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STUDIES ON THE GROWTH OF GORILLA AND OF OTHER HIGHER  
PRIMATES WITH SPECIAL REFERENCE TO A FETUS OF  
GORILLA, PRESERVED IN THE CARNEGIE MUSEUM

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(EIGHT PLATES AND SIX TEXT-FIGURES.)

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## PART I.

## Chapter 1. INTRODUCTION.

The inseparable problems of human evolution and of man's exact place among the primates can be expected to be solved only by a consideration of the findings from *all* the many different fields of science which have evidence to offer for the reconstruction of the pedigree of the primates. The contributions from the various sciences to our knowledge of the higher primates still differ markedly in amount and significance. The prenatal development of the apes ranks probably first among the phases of which least is known to-day. Indeed, much less information is available as to embryos and fetuses of the anthropoids than in regard to fossil apes. Few fetuses of apes have been collected and some of these have either never been described at all, or are merely mentioned in a few words.<sup>1</sup> Still other fetuses have been erroneously identified. Breschet (1845)\* was the first author to deal with what he supposed to be the fetus of a higher ape; he labelled this specimen "*Semnopithecus Hilobates*. Gibbon?". The writer is firmly convinced that this fetus is not that of a gibbon, but one of some short-tailed macaque.<sup>2</sup> On the other hand, the fetus pictured by Darwin (1874) is a gibbon fetus and not that of an orang, as Darwin states, nor that of a chimpanzee, as Schmidt (1892)

\* The dates in brackets refer to the Bibliography, which is appended.

<sup>1</sup> For instance, Lönnberg (1917) lists a chimpanzee fetus in a report on mammals collected in Central Africa; and Prince William of Sweden (1923) mentions that a gorilla fetus was obtained on his expedition, but, as far as the writer is aware, no description of these valuable specimens has appeared as yet. Huxley (1864) devoted only a few words to a chimpanzee fetus; and Anthony (1918), in his detailed description of the brain of a gorilla fetus and of a chimpanzee fetus, gives merely a photograph and a few measurements of the entire specimens.

<sup>2</sup> The upper extremity of this specimen is much too short for a gibbon fetus and the tail would no longer be visible in a gibbon at this stage of development (See Chapter 8, coccygeal tubercle). Several other points support the author's diagnosis: such as the formation of the forehead, of the outer ear, of the foot, and of the placenta.

tried to prove later on.<sup>3</sup> The first thorough description of an anthropoid fetus (orang-utan) is given in the excellent paper by Trinchese (1870). This was followed by Deniker's (1885) classic monograph on a gorilla fetus. To these have since been added a few more or less extensive reports on other ape fetuses; most noteworthy among which are the papers by Schwalbe (1911) and by Bolk (1926 b). The rapid and fundamental changes occurring during intra-uterine life necessitate the study of a great many specimens at different stages of development in order to gain even the barest outlines of prenatal growth. Information on the embryonic period in apes is practically restricted to the one gibbon and one orang embryo described by Keibel (1906). In writing a review of the fetal growth of primates the author (1926 b) collected the few scattered data from the literature and combined these with his own observations in order to give at least a preliminary sketch of some of the fetal conditions in apes.

There can be no doubt that investigations on the ontogeny of the higher primates will be of most essential help in the solution of the problems of primate phylogeny in general and of human evolution in particular, but many more reports on additional material are needed.

In the present paper it is intended first of all to contribute some observations on a new fetus of one of the apes. The author is indebted for this opportunity to Dr. W. J. Holland, who has generously entrusted him with the description of the fetus of a gorilla (Plate I). Since there exist publications on several other gorilla fetuses it seems desirable to discuss them all together and to add to this study of fetal life such data on postnatal growth in the gorilla as are available in the literature and are made possible through an examination of material in various collections. In this attempt to establish the more important changes, which take place during growth in one of the anthropoid apes, it became necessary for a correct interpretation of the findings to compare the conditions in gorilla with those in other representatives of the higher primates. However, these comparisons could not be made as extensive, as might seem desirable, on account of the scarcity of corresponding data on other apes, which will first have to be augmented and subjected to separate study.

<sup>3</sup> Deniker had suspected that this specimen might be a gibbon fetus and not an orang-utan fetus, but Schmidt objected to the "gibbon" determination chiefly on the ground that the ischial callosities were missing. The writer has studied a considerable number of gibbon fetuses and is thus in a position to state that these callosities appear very late in the gibbon (See Chapter 8). The illustration and measurements by Schmidt of the specimen in question agree so closely with the author's data on gibbon fetuses that there can be no doubt of its being a gibbon. Schwalbe was evidently misled by the form of the ear, (which, as Schmidt showed, is due to artificial deformation) in stating that the gibbon fetus, pictured by Darwin, was in his opinion the fetus of a macaque (G. Schwalbe in "Evolution in Modern Thought," Modern Library, New York, p. 119).

The entire investigation is restricted to the characters observable on the outer body and will deal particularly with the body proportions, which are of such outstanding interest in studies of growth. Most of the literature appertaining to growth in gorilla deals with the outer body and its proportions. Of the fetuses of gorilla, for instance, only the specimen of Deniker was actually dissected. The fetus, described for the first time in this paper, belonging to the Carnegie Museum has not been dissected. It was hoped at first that the skeletal system of this specimen could be studied by means of X-ray photographs, but since it had been preserved in formalin for the past sixteen years no satisfactory results could be obtained in that way.<sup>4</sup>

## Chapter 2. MATERIAL.

As mentioned above, a special effort was made in this study to collect from the widely scattered literature those data which have a bearing upon the problem of growth in gorilla. It will be helpful to other students to enumerate here these sources of information and to establish also the age sequence of all the available material. This sequence is chiefly based upon the size of the specimens. Since frequently no measurement of total size has been recorded, the length of the limbs has to serve in such instances as the only possible criterion for the relative age of the specimen.

I.<sup>5</sup> The youngest gorilla fetus on record is the specimen described by Duckworth (1904 a). This fetus is male, and belongs to one of the subspecies of *Gorilla gorilla*. The distance from vertex to coccyx (straight) amounts to 71 mm., the length of the upper arm is 21 mm., and the combined length of thigh and leg equals 30 mm. In its state of development this specimen corresponds most closely to human fetuses of the twelfth or thirteenth week (menstrual age).

II. The gorilla fetus described for the first time in this paper is considerably older than Duckworth's specimen. This fetus is female and corresponds in development to human fetuses of the beginning of the fifteenth week. The distance from vertex to coccyx measures 85 mm., the sitting height is 88.5 mm., the length of the upper arm is 25 mm., and the total length of thigh and leg amounts to 40 mm.

<sup>4</sup> The writer wishes to express his sincere thanks to Dr. E. C. Hill for his persistent and most skilful efforts to obtain good X-ray photographs of this fetus.

The placenta, uterus, and ovaries, which Dr. Holland kindly sent with the gorilla fetus, have been studied by the author's colleagues, Dr. G. B. Wislocki and Dr. C. Hartman, who will report elsewhere on this rare material. (A discussion of this gorilla placenta will appear in a paper by Wislocki, 1927, which is now in press).

<sup>5</sup> Wherever a particular specimen is referred to hereafter these numbers of age sequence will be given. All the specific names in this paper are according to Elliot (1913).

All these surpass the corresponding dimensions of fetus I. This fetus belongs to the Carnegie Museum (Acc. No. 7698) and was collected by the medical missionary, Dr. Hymen L. Weber, in the vicinity of Efulen, Cameroon, in 1910. Dr. Holland has kindly informed the author that this specimen belongs either to *Gorilla gorilla diehli* or to *Gorilla gorilla matschiei*, but that it is assigned with greater probability to the former subspecies.

III. According to its size the gorilla fetus of Deniker (1885) ranks third, corresponding in development to human fetuses of the eighteenth or nineteenth week. This fetus is female, was obtained in West Africa, and hence belongs in all probability to the species *Gorilla gorilla*. The distance from vertex to coccyx measures 135 mm., the upper arm has a length of 53 mm., and the total length of thigh and leg amounts to 82 mm.

IV. The fourth gorilla fetus is that described recently by Bolk (1926 b). Since this author does not state in which part of Africa his specimen was obtained but mentions that it was brought to Amsterdam a long time ago, it can be assumed that it belongs most likely to the *Gorilla gorilla* group and not to the much rarer and more recently discovered East African *Gorilla beringei*. This fetus is male and corresponds in size to human fetuses of the beginning of the sixth month, but in regard to certain other characters of development it seems better comparable to human fetuses of the middle, if not end, of the sixth month. The straight distance from the vertex to the anus amounts in this gorilla fetus to 170 mm., the upper arm is 54 mm. long, and femur and tibia combined have a length of 92 mm.

V. The fifth gorilla fetus is in all probability of the same stage of development as Bolk's specimen; it may be even slightly younger. Unfortunately, Anthony (1918), who described the brain of this fetus, gives only a photograph of the entire specimen (Photograph reproduced on Pl. II, fig. 1) and one of a plaster cast thereof. This fetus is male, came from the French Congo, and belongs, therefore, to one of the subspecies of *Gorilla gorilla*. The distance from the vertex to the coccyx (taken with a tape) is given as approximately 190 mm.; it is to be regretted that no other measurements have been published.

No information of any sort is available in regard to the last part of fetal growth in gorilla.

VI. The next stage in the development of gorilla is represented by the interesting photographs of a gorilla baby published by Reichenow (1921). These pictures were taken at intervals from the age of one month to that of seven months. Reichenow's paper contains no measurements. This specimen was obtained in Cameroon and belongs to the species *Gorilla gorilla*.

VII. The youngest gorilla infant, of which there exist measurements, is the specimen described by Ehlers (1881). It is a male, undoubtedly of the *Gorilla gorilla* group, according to Ehlers less than one year of age, and measures from vertex to coccyx 308 mm. The upper arm length is 114 mm. and the length of thigh and leg amounts to 172 mm.

VIII. Next in age is the female infant (*G. gorilla*) measured by Mollison (1911). From the height of the trunk (208 mm.) and the various indices given by Mollison the upper arm length of this specimen is calculated as 146 mm. and the thigh-plus-leg length as 231 mm. These values are very considerably above the corresponding measurements of Ehlers' infant, thus indicating a marked difference in age between specimens VII and VIII.

IX. The infant described by Deniker (1885) is but little older, *i.e.*, larger, than the infant just mentioned. This specimen is a female with a distance between vertex and coccyx of 405 mm., an upper arm length of 165 mm., and a thigh-plus-leg length of 259 mm. That it must be of the species *Gorilla gorilla* is evident from the fact that the Mountain Gorilla was still unknown at the time of Deniker's publication.

X. Famelart (1883) has published some few measurements on a male gorilla infant, which he kept alive for a few months. According to this author it was captured when about seven months old and had then a sitting height of 320 mm. which is about the same as in infant VII with its distance from vertex to coccyx (somewhat less than sitting height!) of 308 mm. The head measurements were taken by Famelart about three months later, when the animal had attained a size slightly above that of infant IX, judging by its sitting height which had increased to 410 mm. or more (?). This specimen is assigned to the species *Gorilla mayema* Alix and Bouvier, or, as called by Elliot (1913), *Pseudogorilla mayema*.

XI. Information on this stage of growth is available in regard to the proportions of the limbs. These proportions were obtained from measurements on three infantile skeletons of *Gorilla gorilla*. Data for one of these were published by Deniker (1885) and for another by Bolk (1926 b). A third specimen was kindly measured for the author by Dr. W. L. Straus, Jr. in the collection of the Department of Anatomy of Western Reserve University. The lengths of the humeri of these infants average 168 mm. A detailed enumeration of the limb proportions of all the gorilla skeletons, used for this paper, will be found in Table 5. In the tables on growth only the average proportions of these skeletons will be quoted.

XII. The last specimen which could properly be called an infant is the second gorilla (*G. gorilla*) measured by Mollison (1911). From the trunk height

and the proportions of this young female the length of the upper arm is calculated as 212 mm. and the thigh-plus-leg length as 322 mm.

XIII. The juvenile male *Gorilla gorilla*, measured by Bolau (1876), must be considerably older than gorilla XII, since its thigh-plus-leg length amounts to 385 mm. The only other measurement, given by Bolau, which may be used for a determination of relative age, is the combined length of upper arm and forearm amounting to 430 mm. This dimension is calculated as 386 mm. for gorilla XII and amounts to 445 mm. in the next specimen.

XIV. The second juvenile is a male *Gorilla beringei* which the author has studied at the American Museum of Natural History. This specimen was unfortunately skinned and eviscerated so that some measurements could not be taken at all and for the others certain corrections had to be made to allow for the thickness of the skin. These corrections were based upon comparisons between the author's measurements on a chimpanzee of similar age before and after it was skinned. The sitting height of this gorilla amounts to 619 mm., the distance from vertex to coccyx to 587 mm., the upper arm length equals 254 mm., and the thigh-plus-leg length 387 mm.

XV. The average limb proportions of three juvenile skeletons of *Gorilla gorilla* represent the next stage. Data on one of these skeletons were given by Mollison (1911) and on another by Bolk (1926 b). The third skeleton belongs to the collection of the Laboratory of Physical Anthropology, Johns Hopkins University. The average length of the humerus of this series, which is 261 mm., stands between the length of the upper arm of gorilla XIV (254 mm.) and that of gorilla XVI (275 mm.).

XVI. Sommer (1907) has published some measurements on an adult female gorilla ("*Gorilla castaneiceps* Slack" = *G. gorilla castaneiceps*). However, this specimen, which had lived in captivity for seven years, is probably not of normal size for its age, since its sitting height, for instance, measures only 610 mm. The upper arm length of 275 mm. is very little above the humerus length of the juvenile skeletons. The thigh-plus-leg length equals 475 mm. The last two dimensions fall below the range of variation of these measurements in other adult female gorillas (XVII and part of series XVIII). Further remarks on the size of this specimen will be found in Chapter 5. Good photographs of this animal, when alive, have been published by Grabowsky (1906).

XVII. The female *Gorilla gorilla*, described by Ehlers (1881), is the only adult gorilla of typical size in the flesh of which detailed and reliable measurements have been published as far as the author could ascertain. This specimen



had a complete second dentition and all the epiphyseal lines of the long bones were obliterated. The distance between vertex and coccyx is given as 700 mm., the upper arm length as 339 mm., and the thigh-plus-leg length as 535 mm.

XVIII. In order to place at least some of the proportions in adult gorilla on a more representative basis than is afforded by the above specimens alone, the average limb proportions of 38 adult skeletons of West African gorillas (*G. gorilla* and its various subspecies?) have been figured from data in the literature and from measurements of specimens in various collections. Publications of the following authors were consulted in assembling this series: Du Chaillu (1861) one skeleton; Deniker (1885) one skeleton; Mollison (1911) sixteen skeletons; Lorenz v. Liburnau (1917) three skeletons; and Bolk (1926 b) two skeletons. In addition measurements by Dr. W. L. Straus, Jr. on five skeletons in the collection of the Western Reserve University were incorporated and also the results of the author's examination of nine skeletons in the collections of the U. S. National Museum, the American Museum of Natural History, the Department of Zoology of Columbia University, and the Anthropological Laboratory of Johns Hopkins University, as well as of one skeleton from West Africa, measured some time ago in a dealer's store in Berlin.

In order to test the question whether there are any specific differences between the proportions of *Gorilla gorilla* and *Gorilla beringei*, five adult skeletons of the latter type were measured by the author and their limb proportions compared with those of the above series XVIII. Four of these rare skeletons of the Mountain Gorilla are from the American Museum of Natural History and one from the National Museum. For the purpose of certain further comparisons use was made of measurements by Lorenz v. Liburnau (1917) on the limb bones of five adult Mountain Gorillas of the species *Gorilla graueri* Matschie.

Two stages of the growth of gorilla were selected for detailed comparison with representatives of the other higher primates at corresponding ages. The first stage is given by the fetus (II) of the Carnegie Museum, the only specimen of prenatal growth of which a complete set of measurements is available. The second stage was chosen to represent the completion of growth, *i.e.*, adult life. The special technique employed for these comparisons required observations on a considerable number of individuals of at least one of the higher primates in order to establish some measure for range of variation. A larger series of cases of the same age is available for man only. The following material, or papers describing certain material, was assembled for these comparisons:

*For the stage of fetal growth:*

1. Twenty human fetuses (white) from the end of the fourteenth and the beginning of the fifteenth week, ranging in sitting height from 85 to 92 mm., with an average sitting height of 88.5 mm., *i.e.*, exactly the same as in gorilla fetus II.

2. The youngest chimpanzee fetus on record is that described by Friedenthal (1914). This specimen is somewhat larger than gorilla fetus II, but is the only one which can serve for comparison. The distance from the vertex to the symphysis pubis is obtained as 99 mm. by adding certain measurements given by Friedenthal. This dimension corresponds to a sitting height of approximately 110 mm. Judging by the photograph of this specimen, its stage of development can not differ very markedly from that of gorilla fetus II.

3. Of the four orang-utan fetuses, of which measurements have been published by Schwalbe (1911), specimen No. 3 agrees in its size most closely with gorilla II. The vertex-coccyx length, taken with a tape, amounts in both to 115 mm., the greatest head length is in the orang 35 mm. and in the gorilla 34.1 mm. It can be assumed that the sitting height (straight measurement) of this orang fetus must be also very similar to that of the gorilla fetus, *i.e.*, approximately 88.5 mm.

4. A gibbon fetus (*Hylobates concolor*) of a stage of development corresponding to that of gorilla II was measured by the author. This specimen belongs to the collection of the late Prof. E. Selenka (No. 24 a). It has a sitting height of 56 mm.

*For the stage of adult growth:*

5. Twenty-four adult white men from eighteen to twenty-five years of age. These adults, as well as the above mentioned human fetuses (Series 1), had been measured by the author in connection with his extensive investigations on human growth. Full details on these series will be published in a later paper.

6. Measurements on a fully adult chimpanzee have been published by Friedenthal (1914). This specimen is a female, weighing 55 kgm.

7. An adult orang-utan in a perfect state of preservation was measured by the author at the American Museum of Natural History (Department of Comparative Anatomy, No. 563). This ape is a female and has a sitting height of 717 mm.

8. The adult gibbon used in this paper was also measured by the author. This specimen is of the same species (*Hylobates concolor*) as fetus 4 and belongs also to the Selenka collection (No. 16 a). It has a sitting height of 237 mm.

The author wishes to take this opportunity to express his sincere thanks to Mrs. E. Selenka, Prof. W. K. Gregory, Prof. J. H. McGregor, and Mr. G. S. Miller, Jr., for their ready and generous permission to study the valuable material mentioned above. The writer is furthermore indebted to his former student, Dr. W. L. Straus, Jr., who kindly measured for him the gorilla skeletons in the collection of Western Reserve University, and to Prof. T. W. Todd, who very obligingly permitted this.

## Chapter 3. TECHNIQUE.

The measurements taken on this primate material correspond, wherever possible, to those generally used in anthropometry (See Martin, 1914). Many measurements have to be taken in order to express accurately the dimensions

and proportions of every part of the body. It is very essential that such measurements are defined precisely, so that the recorded data are not open to misinterpretation. Unfortunately it is often very difficult, and sometimes impossible, to make use of some measurements given in the literature, simply because authors have omitted to state their methods of measuring.

The following list of measurements explains the technique adopted by the author. The diagram on Pl. III, fig. 1 obviates a detailed description of many dimensions. The specimen, no matter of what age, is first placed flat on its back with its spine practically straight and its head posed so that an imaginary plane, determined by the ear openings and the lowest point of one orbit (ear-eye horizon), stands perpendicular to the body axis. All the "height" measurements on the trunk and the head are taken strictly parallel to the body axis, as represented by the table on which the specimen rests.

*General measurements:*<sup>6</sup>

1. Sitting height: from vertex to buttocks over ischial tuberosities (See Pl. III, fig. 1).
2. Stature: can be taken directly only in man after birth. In all primate fetuses and in all apes the knees are flexed so that the approximate stature is best obtained by the addition of measurements 3, 16, and 17.
3. Cephalo-thoraco-abdominal height: vertex to upper edge of symphysis pubis (symphysis).

*Trunk measurements:*

4. Anterior trunk height: suprasternal notch to symphysis.
5. Acromion height: middle of line connecting the lateral points on acromial processes of shoulder blades (acromion) to symphysis.
6. Shoulder height: projective height of acromion over suprasternal notch (obtained by subtraction of m. 4 from m. 5).
7. Nipple height: middle of line connecting centers of nipples to symphysis.
8. Umbilicus height: center of attachment of umbilical cord or center of umbilical scar to symphysis. This measurement can not be taken in many adult apes, since they frequently have no trace of an umbilical scar left.
9. Shoulder breadth: distance between right and left acromion.
10. Hip breadth: distance between most lateral points over the great trochanters.
11. Nipple breadth: distance between centers of nipples.
12. Transverse chest diameter: at level of sternal attachment of fourth pair of ribs.
13. Sagittal chest diameter: at same level as m. 12.
14. Chest circumference: at same level as m. 12 and m. 13.

*Limb measurements:*

15. Total lower limb length: obtained by addition of m. 16 and m. 17.
16. Thigh length: length of femur taken laterally from top of great trochanter.
17. Knee—sole length: length of tibia plus foot height, taken medially.
18. Leg length: length of tibia to tip of internal malleolus.

<sup>6</sup> Wherever the absolute measurements are referred to hereafter their serial number will be given together with the letter *m* to distinguish them from the relative measurements, or indices, the numbers of which will be accompanied by an *i*.

19. Foot length: from heel to tip of longest toe.
20. Great toe length: from heel to tip of hallux (hallux adduced).
21. Foot breadth: greatest width between metatarso-phalangeal joints of toes II to V.
22. Total upper limb length: obtained by addition of m. 23, m. 24, and m. 25.
23. Upper arm length: length of humerus from acromion to humero-radial joint.
24. Forearm length: length of radius to tip of styloid process.
25. Hand length: from middle of line connecting tips of ulnar and radial styloid processes to tip of middle finger.
26. Thumb length: from styloid process of radius to tip of thumb (thumb adduced).
27. Hand breadth: greatest width between metacarpo-phalangeal joints of fingers II to V.

*Head measurements:*

28. Average head diameter (head module): sum of m. 30, m. 32, and m. 33 divided by 3.
29. Average head circumference: arithmetic mean of the three circumferences in the three different dimensions, *i.e.*, sum of m. 34, (m. 35 + m. 31), and (m. 36 + m. 37) divided by 3.
30. Head length: greatest length of brain part of head (from glabella).
31. Nasion—inion length (base length): point overlying middle of naso-frontal suture (nasion) to occipital protuberance (inion), measured in a straight line.
32. Head breadth: greatest breadth of brain part of head between parietals or temporals.
33. Head height: upper end of tragus (tragion point) to vertex, projective height perpendicular to ear—eye horizon.
34. Horizontal head circumference: at level of m. 30.
35. Sagittal arc of head: distance between the two end points of m. 31, taken with tape.
36. Transverse arc of head: distance between the two tragion points, taken with tape over vertex.
37. Biauricular breadth (base breadth): distance between the end points of m. 36, taken in a straight line.
38. Total head height: from chin to vertex.
39. Total face height: from chin to nasion.
40. Upper face height: from middle of mouth to nasion.
41. Face breadth: width between most lateral points over zygomatic arches.
42. Nose height: from nasion to lowest point on nasal septum.
43. Nose breadth: greatest width between nasal wings (in some of the apes impossible to determine exactly).
44. Interocular breadth: distance between inner angles of eye-clefts.
45. Biocular breadth: distance between outer angles of eye-clefts.
46. Mouth breadth: greatest horizontal width of closed mouth, measured in a straight line.
47. Ear height: greatest height of outer ear.
48. Ear breadth: greatest width of outer ear, perpendicular to m. 47.

With these measurements it is possible to construct complete and very accurate diagrams of the body proportions of any specimen, as shown, for instance, on Pl. III, fig 2.

A few additional measurements had to be taken solely in order to render the author's material directly comparable to certain data in the literature. These substituted measurements, which had to be used in some of the tables, are the following:

- 1a. Vertex—coccyx length (somewhat smaller than sitting height).
- 9a. Deltoid breadth: greatest width between deltoid muscles (somewhat larger than shoulder breadth).
- 10a. Pelvic breadth: greatest distance between iliac crests (differs from hip breadth in varying degree).
- 28a. Average head diameter: considering only head length and head breadth, but not head height, as does m. 28.

From these absolute measurements, which are always given in millimeters, a series of proportions or indices is formed, in which the measurements are invariably expressed in percentage of one another. A considerable number of these relative measurements are not ordinarily adopted by the author. Their selection for this study was largely governed by the particular measurements, available in the literature, which often left no choice for other and more significant proportions. Since most authors have recorded but few measurements there will be unfortunately frequent gaps in the tables of indices.

A number of evident errors were detected among the measurements available in the various publications on gorilla and other apes. At times these errors could be corrected,<sup>7</sup> but more often the doubtful data had to be discarded. On the other hand, in some cases it was possible to calculate certain essential measurements from published figures for other dimensions of the same specimen.<sup>8</sup>

#### Chapter 4. GORILLA FETUS II.

All the absolute measurements and a few other data on the gorilla fetus of the Carnegie Museum are recorded in this preliminary chapter. The proportions and many other features of this specimen will be discussed together with all the other material in the later chapters.

Plate I gives two general views of the fetus as it was fixed by preserving fluid in the natural position which it maintained in the uterine cavity. This particular position, which very closely resembles that of the average human

<sup>7</sup> For instance, Friedenthal (1914) gives the thigh length of a chimpanzee fetus (2) as 24.5 mm. and the leg length of the same specimen as 27 mm.; these two figures undoubtedly have been reversed by the printer, since no chimpanzee has a greater length of the tibia than of the femur. In the same way the head length and breadth of Friedenthal's adult chimpanzee (6) should be reversed, since no ape has a head length of 191 mm. combined with a breadth of 257 mm. The gorilla fetus III can not have an anterior trunk height of only 54 mm. and an umbilicus height of 24 mm., as stated by Deniker, but, judging by the excellent photographs in natural size of this specimen, the former measurement must be at least 59 mm. and the latter not more than 12 mm. Deniker's two figures resulted in impossible proportions, but from the latter, carefully corrected figures, indices are obtained, which do not remove this specimen too far from the other gorilla fetuses. Of this same fetus III Deniker has published the measurements of the long bones of the limbs as well as those of upper arm, forearm, etc. Since these two sets of supposedly closely corresponding measurements agree but slightly (*e.g.* leg length = 33 mm., tibia length = 35 mm.; thigh length = 49 mm., femur length = 44 mm.) the writer has used Deniker's skeletal measurements wherever possible.

<sup>8</sup> For instance, among Ehlers' (1881) measurements on two gorillas (VII & XVII) are listed the distances from vertex to suprasternal notch and to symphysis, by subtraction of the former from the latter distance the anterior trunk-height is obtained. By similar methods it was possible to calculate from available figures certain additional measurements for the specimens of Ehlers, Sommer, and Mollison.

fetus seems to be maintained by gorilla with little variation throughout at least the middle of its fetal life. The text-figures given by Deniker show that the specimen of that author had its head and limbs flexed in a very similar manner. The older gorilla fetuses of Bolk and of Anthony (See Plate II, fig. 1) are bent even more than fetus II. It is particularly noteworthy that in all these fetuses the feet are posed so that their soles stand in almost parallel planes, facing one another. In human fetuses of the same growth period the feet have moved much further downward and the tibiæ are rarely directed transverse to the body axis, as in the gorilla fetuses.

The umbilical cord of fetus II, which has a length of 156 mm., is very little twisted and was not wound around the body, as in Bolk's specimen.

Table 1 compares the absolute measurements of gorilla fetus II with the corresponding average dimensions on human fetuses of the same stage of development.

TABLE 1.

Absolute measurements (in mm.) of Gorilla Fetus II and of Human Fetuses (Series I, average) of corresponding development.

No. of Measurements	Gorilla Fetus II.	Human fetuses	No. of Measurements	Gorilla Fetus II.	Human fetuses
1. Sitting height.....	88.5	88.5	25. Hand length.....	20.0	12.0
2. Stature.....	123.3	124.3	26. Thumb length.....	9.6	8.8
3. Cephalo-thoraco-abdom. h.....	79.5	79.6	27. Hand breadth.....	7.8	6.5
4. Anterior trunk height.....	40.6	38.4	28. Average head diameter.....	29.4	29.7
5. Acromion height.....	48.4	41.2	29. Average head circumference....	96.8	101.0
6. Shoulder height.....	7.8	2.8	30. Head length.....	34.1	33.5
7. Nipple height.....	34.0	29.8	31. Nasion—inion length.....	33.0	30.6
8. Umbilicus height.....	8.5	6.6	32. Head breadth.....	31.0	29.3
9. Shoulder breadth.....	29.6	25.6	33. Head height.....	23.2	26.2
10. Hip breadth.....	18.8	18.7	34. Horizontal head circumference..	102.0	101.6
11. Nipple breadth.....	16.9	15.2	35. Sagittal arc of head.....	60.3	72.7
12. Transverse chest diameter.....	29.2	26.2	36. Transverse arc of head.....	65.2	72.6
13. Sagittal chest diameter.....	26.8	21.8	37. Biauricular breadth.....	30.0	25.7
14. Chest circumference.....	94.0	79.0	38. Total head height.....	34.3	35.5
15. Total lower limb length.....	43.8	44.7	39. Total face height.....	16.4	13.7
16. Thigh length.....	22.6	23.4	40. Upper face height.....	12.7	9.1
17. Knee—sole length.....	21.2	21.3	41. Face breadth.....	26.7	24.7
18. Leg length.....	17.8	17.7	42. Nose height.....	9.0	6.2
19. Foot length.....	19.0	14.4	43. Nose breadth.....	12.0	6.3
20. Great toe length.....	16.9	13.8	44. Interocular breadth.....	7.6	8.5
21. Foot breadth.....	6.0	4.4	45. Biocular breadth.....	18.6	18.6
22. Total upper limb length.....	66.3	50.8	46. Mouth breadth.....	12.0	8.6
23. Upper arm length.....	25.0	22.2	47. Ear height.....	9.0	7.1
24. Forearm length.....	21.3	16.7	48. Ear breadth.....	6.1	4.2

The chief results from this comparison are illustrated on Pl. III, fig. 2. It is first of all apparent that the gorilla, though of identical sitting height and almost the same stature as the average of the human fetuses, is much more bulky than the latter. This is best shown by the difference in body weight, that of the

gorilla being 64.2 gm. whereas the average weight of the human fetuses is only 50.6 gm. That the chest in the gorilla fetus is proportionately wider than in the human fetus is evident from a comparison between the shoulder breadth, chest circumference, and chest diameters of the two (See Table 1). The gorilla fetus, when contrasted with human fetuses, is furthermore characterized by long upper limbs, long and slender hands and feet, and a large face. The brain part of the head is slightly longer and broader but much lower in the gorilla than in the human fetus. The neck of the former is strikingly thick and short, a condition which appears emphasized through the extremely high location of the shoulder (See Pl. III, fig. 2). Most of these features represent indications of the much more marked differences which exist between adult gorilla and man.

## PART II.

### Chapter 5. RATE OF GROWTH.

There exist but meagre data bearing upon the duration of the various phases of growth in the higher apes, so that little can be said in regard to the important problems of their rate of growth and the possible fluctuations thereof. Deniker (1885) supposes that the duration of pregnancy in anthropoids varies between eight and nine months. According to v. Allesch (1921) a pregnant chimpanzee menstruated until five months before she gave birth to a baby, but he does not consider this conclusive, since he states: "Man hat also die Wahl, eine Tragzeit von nur 5 Monaten anzunehmen oder mit der Möglichkeit zu rechnen, dass die Blutung auch noch beim tragenden Tier ein oder mehrere Male weiterdauert." There can be no doubt that pregnancy in the large apes extends over a longer period than five months since Cuvier found it to last seven months in such low forms as macaques. Bolk (1926 b) assumes that gestation in gorilla is shorter than in man, since the former weighs at birth considerably less than the latter. However, the size of the fetus at term is among different primates apparently not correlated with the duration of their intra-uterine growth, as is shown by the following facts. Pregnancy in man lasts nine months and the birth weight is about six or seven pounds. In a captive chimpanzee Montané (1916) found the duration of gestation to be also nine months, although the weight of a newborn chimpanzee is only little above two pounds (Blair, 1920). Since the prenatal life of the chimpanzee has been established by Montané as being of the same length as in man, it can hardly be assumed that the gorilla would differ in this respect. Reichenow (1921) captured a gorilla baby (VI), only a few days old, which weighed two

kilograms. Bolk's gorilla fetus weighs exactly one pound and, therefore, must be still far from term.<sup>9</sup>

Body weight varies very considerably at any age in man and, apparently, also in gorilla. For instance, the male gorilla baby (X), captured by Famelart, was in this author's opinion about seven months old, yet it weighed only two kilograms, *i.e.*, as much as Reichenow's new-born. Of course, the above estimate of age may be too high, but the animal must have been at least two months old, since two incisors had erupted in the upper jaw and four in the lower jaw. Akeley (1923) gives the following interesting quotation from a letter by an English hunter: ". . . shot a female [Mountain Gorilla] with a young one in her arms . . . The baby was apparently not more than 24 hours old . . . The baby gorilla (a female) is now two months old and in the best of health and weighs nine pounds. She has cut six teeth. She does not show any signs of walking yet . . ." <sup>10</sup> Considering the reports by the last two authors, it seems most probable that the average weight of the gorilla at birth is even somewhat less than that of Reichenow's new-born, and certainly less than the average weight in man at birth, but more than that of the chimpanzee. Since the periods in which these birth weights are acquired are in all likelihood the same for man and the higher apes, it may be concluded that the average rate of prenatal growth is less in the gorilla and the chimpanzee than in man.

During early infancy the chimpanzee continues to lag behind man in its weight. According to Yerkes (1925) a chimpanzee, born in Cuba, weighed at the age of two years only twelve pounds, and it is stated to be a "remarkably healthy, well-nourished, and altogether normal individual." During later infancy and childhood some chimpanzees grow more rapidly as shown by the following figures, mentioned by Heck (1916): One chimpanzee increased in weight during five years from eleven to twenty-three kilograms, another one grew in the same interval from seven and one-half to twenty-five kilograms, and a third animal multiplied

<sup>9</sup> The gorilla fetus V is at practically the same stage of development as Bolk's specimen (IV); both correspond to human fetuses of the sixth month. Anthony (1912) has published two photographs of the mother animal of fetus V, taken immediately after her death. Judging by these illustrations, which show a tremendously enlarged abdomen, even this relatively early stage of pregnancy is most conspicuous in the gorilla. It is easily as noticeable as in man and apparently more so than in the chimpanzee, since v. Allesch (1921) reports that the appearance of a pregnant chimpanzee in the Berlin Zoological Garden did in no respect begin to change until two months before the birth of her young. Even during this last period, when her abdomen became enlarged, it never protruded beyond the chest and, incidentally, her breasts remained unaltered in size.

<sup>10</sup> The captive gorilla baby of Reichenow (1921) made the first attempts at walking at the age of seven and a half months, as shown by interesting photographs in this author's publication.



its initial weight even almost four times in four years, namely from fifteen to fifty-eight kilograms—an astoundingly rapid gain.

No gorilla has ever been born in captivity, so that the determinations of age for this ape are always rather roughly estimated. The author had an opportunity to examine the young male West African gorilla "John Daniel II" in May 1924. At that time this ape was said to be about four to four and a half years old; it had an approximate standing height of 106 cm. and weighed about eighty pounds. Yerkes (1927) mentions that the female Mountain Gorilla "Congo", studied by him, had an approximate age of four to five years, weighed about sixty-five pounds, and had a standing height of 96.5 cm. ( $\pm 2.5$  cm.). These data indicate that gorillas must grow rather rapidly, at least during the later part of infancy. This is also borne out by the following records: Famelart's male gorilla baby (X) measured 32 cm. from vertex to anus at the time it was captured, when it was said to be about seven months old. After only two months this dimension had increased to 41 cm. A young male gorilla, kept alive for two years by Falkenstein, increased in weight during that time from fourteen to twenty-one kilograms (quoted by Heck, 1916). According to Hornaday (1922) the young gorilla "John" (= "John Daniel I"?), when purchased in London, weighed thirty-two pounds. Two years and three months later it had reached the weight of one hundred and twelve pounds, *i.e.*, three and a half times the initial weight. A very much slower increase occurred in the female gorilla (XVI), which lived for over seven years in the Zoological Garden of Breslau. This animal had, when received, an estimated age of about four years, and weighed thirty-one and one half pounds. During the first four years of captivity it grew in weight only to sixty pounds (Grabowsky, 1906), which is very little even for a female and arouses the suspicion that the animal (though stated to be perfectly healthy) may have been kept on an insufficient diet, or without adequate exercise or sunlight.

The duration of the total postnatal growth period in the higher apes is known with certainty only in the case of the chimpanzee. Sir Edwin Ray Lankester (1915) states that the female chimpanzee "Sally" at the London Zoological Garden was full-grown and adult at the age of eight years. The mother of the first chimpanzee born in New York (*Pan chimpanse*) was ten years old and the father (*Pan schweinfurthi*) had an approximate age of eight years (Blair, 1920). Mitchell (1912) is of the opinion that the period of growth in anthropoid apes lasts eight to twelve years. The above mentioned female gorilla from Breslau showed undoubted signs of sexual maturity at the age of five years, and grew very little (only six pounds) from the age of eight years to her death at eleven years, so that she was quite

mature and full-grown at eight years, provided that the estimate of four years as the age of her capture is correct.

A few figures will suffice to give an approximate idea of the weight of the body in adult apes. According to Bauman (1926) the full-grown female chimpanzee "Suzette" of the New York Zoological Park weighed one hundred and thirty-five pounds and her male companion, "Boma," had a weight of one hundred and sixty-five pounds. The large female chimpanzee "Johanna" of the Zoological Garden in Philadelphia weighed at the time of her death one hundred and sixty pounds. The writer has been assured by experienced and reliable dealers in animals that some male chimpanzees may attain a much greater weight than the figures above quoted.

It is well known that adult gorillas are very much heavier than adult chimpanzees. Akeley (1923) gives the weight of an adult male as three hundred and sixty pounds, and Prince William of Sweden (1923) quotes three hundred and thirty pounds for a full-grown male gorilla. Even much higher figures are found in the literature, but these are mostly estimates, and not actual weights, as in the above two cases. For instance, Heck (1916) mentions a giant gorilla, which was killed by H. Paschen in 1900 in Cameroon. This specimen, which is now in the Tring Museum, is reported to have a standing height of over two meters and a "conservatively estimated" weight of two hundred and fifty kilograms!

From these notes it may be concluded that at the completion of growth the chimpanzee is nearly or quite as heavy as man and that the gorilla greatly surpasses man in bulk. Since the final weight in apes is attained in considerably less time than in man (in only eight or ten years), and, since the weight at birth of the apes (chimpanzee slightly over two pounds, gorilla four pounds) is less than in man, the general intensity and rate of postnatal growth must be much higher in these apes than in man. This rate is particularly striking in the gorilla, which may increase in weight from four pounds or less at birth, to three hundred and sixty pounds and more, in adult life, and this during as short a period as eight to ten years. It is very interesting and significant to find that the gorilla, according to all available data, grows more slowly than man before birth, but much more rapidly than man during postnatal life.

#### Chapter 6. PIGMENTATION.

Gorilla fetus I is entirely unpigmented, since Duckworth states that its skin is uniformly whitish. The only pigmentation of the next oldest specimen, fetus II, occurs on the ears, which are of a light brown color (See Pl. I), in striking contrast

to the rest of the body, which is still absolutely white. It may be mentioned here that Schwalbe (1911) found in a somewhat older fetus of orang-utan the ears, the nasal bridge, and some parts in the pelvic region a much darker brown than the remaining surface of the body. It seems, therefore, that pigmentation in the anthropoids begins in localized zones, similar to the condition in the negro, in whom the first pigment appears on the scrotum. Deniker's gorilla fetus (III) is of a light brown color, except the face, palm, and sole, which are more of a yellowish tone; the darkest pigmentation is found on the back. It is interesting that fetus IV, which is considerably older than Deniker's specimen, is according to Bolk less pigmented than the younger fetus. This fact indicates a variability in the age of beginning pigmentation in gorilla similar to that observed by the author in negro fetuses, in which, however, the skin commences to darken at a later stage of development. Bolk states that the color of the skin of his gorilla fetus is not much different from that of a white human fetus, except that one can detect an indication of yellow and on the back a faint brownish tint. Reichenow's gorilla baby showed at the approximate age of one month a still fairly light chocolate-brown color (See Pl. II, fig. 3), which, however, darkened very rapidly, having in the third month turned into black. Du Chaillu (1861) states that the color of the skin of young and of adult gorillas is intense black.

In the chimpanzee the pigment of the skin apparently develops sooner than in the gorilla. The chimpanzee fetus (*Pan kooloo-kamba*) of Friedenthal (1914), which has a total weight of only three hundred and seventy grams, already shows a rather dark skin and perfectly black hair (Friedenthal, 1908 a). Bolk's (1926 b) chimpanzee fetus, which weighs six hundred and sixty grams, has a much darker skin than the slightly younger gorilla fetus of the same author. The excellent photograph by Anthony (1918) of an older chimpanzee fetus ("*Anthropopithecus Tschego* Duv." = *Pan satyrus* ?), measuring from vertex to coccyx 250 mm., shows a skin, which seems to be considerably darker than even that of Reichenow's gorilla baby at the age of one month. This last mentioned gorilla appears to be lighter also than the new-born chimpanzee, described by Blair (1920), which, however, was not yet as dark as a chimpanzee baby weighing six and one half pounds, and about a year, or less, old.<sup>11</sup> The author is convinced that at this stage of growth, or sooner, the skin of chimpanzee is in general as dark as it ever becomes, since none of the many older chimpanzees examined by him had developed darker hues. Certain parts of the skin, particularly over the face, ears, chest,

<sup>11</sup> Prof. McGregor kindly permitted the author to examine this specimen. The preserved body of the new-born chimpanzee, mentioned above, was generously lent to the writer by the late Prof. Huntington.

palms, and soles, remain in many species of chimpanzee rather pale throughout life, while other parts may become somewhat darker in their pigmentation but only few species have really very dark skins, comparable to those of gorillas.

These notes, together with the author's observations on the color of the skin in extensive series of negro fetuses and infants, permit the conclusion that pigmentation begins in chimpanzee at an earlier stage of development than in gorilla, the latter being intermediate in this respect between the former and the negro. In all three forms the final and darkest pigmentation is not reached until some time after birth.

Bolk (1917) found deep blue pigmented areas, of a nature identical with the so-called Mongolian spots in man, over the iliac crests of his chimpanzee fetus, which corresponds in development to human fetuses of the sixth, or at most seventh month. The writer has never found any Mongolian spots in human fetuses of that age, but has observed them frequently in white as well as negro fetuses close to term. This difference serves as a further support for the conclusion that pigment develops earlier in the ape than in man. In orang-utan the coloring of the skin appears at least as early as in the chimpanzee and hence also very much sooner than in man. Schwalbe (1911) reports that an orang fetus (No. 3, Chapter 2), which is of the same stage of development as gorilla fetus II, has a brownish color on the entire body.

To these notes on pigmentation must be added the remark of Famelart (1883) that the color of the eye of his infant gorilla changed during one month from yellow to chestnut-brown.<sup>12</sup> Finally, it may be mentioned that the literature contains several reports, which claim that the color of the hair of gorilla changes at least locally during childhood and again during old age. The hair itself develops some time before any pigment appears in it, since all the hairs of gorilla fetus II are absolutely colorless, whereas in fetus III they are pigmented.

#### Chapter 7. HAIR.

The prenatal development of hairs is strikingly similar in anthropoid apes and man. Gorilla fetus I does not as yet show any hair at all. The first hair, which appears in fetus II, must be described in some detail. Faint indications of hair follicles can be detected under a magnifying glass on most parts of the body, but macroscopically visible hair is present only on the eye-brows, lips, and chin, *i.e.*,

<sup>12</sup> Some shade of medium dark brown seems to be the normal color of the iris in juvenile gorillas. It was noted by the author on the young gorillas "John Daniel II" and specimen XIV. Friedenthal (1910), moreover, gives a colored illustration of a young gorilla with a brown iris. The adult gorilla XVI had according to Heine (1906) a dark brown iris. Hartmann (1889), too, mentions that the iris of the gorilla darkens with age.

on the same places as in human fetuses (See Pl. VIII, Fetus II). The slightly more than two hundred hairs of the region of the eyebrows meet in the midsagittal plane, but are much shorter in the glabellar zone than above the eyes. In the middle portion all the hairs point straight upward, but towards the sides they diverge laterally, assuming finally a horizontal direction. The hairs on the upper lip diverge sharply from the center, pointing slightly upward near the mid-line, but changing gradually to a slightly downward direction above the corners of the mouth. All the hair on the lower lip and chin is directed downward. Since none of these hairs exceed 0.33 mm. in length, their direction was determined on enlarged photographs.

In gorilla fetus III the eyelashes have appeared; the hair on the eyebrows has reached a length of 5 to 7 mm.; the hair on the scalp is fairly well developed, though still short; and many parts on the trunk and limbs bear a coat of very short hair. (Many further details are given by Deniker, 1885). Bolk (1919 and 1926 b) has published exhaustive reports on the hair of gorilla fetus IV and on that of a slightly older chimpanzee fetus. One of the most interesting findings on these two specimens is the fact that the hair on their scalp is very much longer than on the rest of the body. In the gorilla it extends down to the eyebrows, whereas in the chimpanzee it leaves the forehead practically bare. In a younger chimpanzee fetus Friedenthal (1908 a) had already found this striking condition, and states that the body was covered with fine and extremely short hair, but that strong black hair of very considerable length extended over exactly the same area of the top of the head as in man. The chimpanzee fetus, pictured by Anthony (1918), shows surprisingly long black hairs on top of the head, but very little hair on the rest of its body. Montané (1916) states that the chimpanzee, born in Cuba, was at birth "completely hairless" with the exception of the head, the scalp bearing abundant hair. The new-born chimpanzee, shown on many illustrations by Blair (1920), likewise has the longest hair on the scalp, but in addition the outside of the limbs and the back already bear hair of considerable length. However, that there are chimpanzees in which the hair of the body in general does not attain any noteworthy length until a considerable time after birth, is proved by the baby from Cameroon, pictured by Matschie (1919). This chimpanzee is practically naked, except for long hair on the crown of its head and the sides of its face. Only its middle incisors have erupted, so that it must have been two months old, since in the above mentioned Cuban chimpanzee these teeth did not appear until two months after its birth. Data for still later growth changes in the hair of chimpanzee (*Pan schweinfurthi*) are given in the following instructive quotation from Allen

(1925): "In the youngest specimen, in which the incisors and canines are only beginning to break through the gums,<sup>13</sup> the whole underside of the body and inside of the limbs is nearly naked and pale yellowish brown like the face. The whole head is heavily clothed with black rather soft hair about 25 mm. long; the rest of the upper parts are thinly haired, the skin showing through; the hair is much shorter and thinner than on the head. At a later stage (milk dentition, m<sup>1</sup> not fully mature) the body is well clothed . . ." Further information on the hair changes in the apes is contained in the following quotation from v. Allesch (1921) appertaining to a chimpanzee, born in the Zoological Garden in Berlin: "Das erste Haar [at birth] war sehr lang, schlicht, völlig schwarz, am Kopf klar gescheitelt. Am Ende der vierten Woche ging es aus. . . Schon in der nächsten Woche kam das neue Haar, das anfangs kürzer blieb und einen leichten Stich ins Bräunliche aufwies."

The gorilla baby VI was, when captured, very sparsely covered with hair, appearing almost naked, but on the crown of its head there arose a tuft of very long brown hair (See Pl. II, fig. 3). Within a few months the body was covered with a dense coat of hair, extending also over the forehead, which at first was entirely bare.

As yet unfinished studies of the author on large series of fetuses, new-borns, and infants of monkeys permit the preliminary and very generalized statement that there exists a greater difference in the conditions of growth of the hair between the monkeys and the anthropoid apes than between the latter and man, except, of course, in late stages of growth.

#### Chapter 8. TRUNK.

All the available data for changes of growth in the proportions of the trunk in the gorilla are listed in Table 2. A glance at this table with its many gaps in the rows of figures makes it at once apparent that as yet but little can be definitely said in regard to the growth of the trunk. The ontogenetic changes in some of the most important proportions of the trunk can not be studied at all, since the necessary measurements were not taken on their material by other authors. There can be no doubt that there exists a very pronounced variability in gorillas, so that part of the irregular age-changes in the indices of Table 2 may be accounted for on that basis. However, it has also to be borne in mind that some of the measurements in the literature, from which indices have been formed, may not have been taken accurately, or at least not in exactly the same way as supposedly

<sup>13</sup> Judging by the teeth, this specimen must be several months old and not, as Allen states, "apparently only a few days old." The lateral incisors in the above mentioned Cuban chimpanzee baby did not erupt until the third month.

corresponding measurements by other authors. Table 2, and the other following tables on growth, do not pretend to show detailed ontogenetic changes based on typical figures, but represents rather a first attempt to gain some preliminary idea of the general trend of certain proportions during advancing age.

TABLE 2.  
Growth Changes in the Proportions of the Trunk of Gorilla.

Index No.	Percentage relation between:	Fetus	Fetus	Fetus	Infant	Infant	Infant	Infant	Juv.	Juv.	Adult	Adult
		I	II	III	VII	VIII	IX	XII	XIII	XIV	XVI	XVII
1.	Chest circumfer. (m.14) & Trunk h. (m.4)	221.2	231.5	281.5	....	....	....	....	....	171.6	180.0	....
1 a.	Chest circumfer. (m.14) & Stature (m.2)	83.0	76.2	84.7	....	....	71.0	....	76.9	62.6	69.9	....
2.	Shoulder br. (m.9) & Trunk h. (m.4)	....	72.9	....	64.1	....	....	70.0	....	61.9	....	60.8
2 a.	Deltoid br. (m.9a) & Trunk h. (m.4)	....	83.3	93.1	121.9	....	....	....	....	....	77.5	....
3 a.	Pelvic br. (m.10a) & Trunk h. (m.4)	....	60.6	54.9	79.7	59.9	62.0	....	71.0	....	54.9	....
4 a.	Pelvic br. (m.10a) & Shoulder br. (m.9)	....	75.3	....	103.7	....	....	101.3	....	88.7	....	106.1
4 b.	Pelvic br. (m.10a) & Deltoid br. (m.9a)	....	72.7	59.0	65.3	....	....	....	....	....	....	....
7 a.	Nipple br. (m.11) & Trunk h. (m.4)	....	33.3	41.6	54.2	32.3	....	....	36.0	....	....	....
8.	Nipple h. (m.7) & Trunk h. (m.4)	....	83.7	....	....	....	....	....	83.0	....	....	....
9.	Umbilicus h. (m.8) & Trunk h. (m.4)	....	18.2	20.9	20.5	....	....	....	27.0	....	....	15.0 17.8

The chest circumference decreases in relation to the trunk height (i 1) as well as in relation to the stature (i 1a) as growth proceeds, a change which agrees very closely with that in most other primates, including man (See Schultz, 1926 b). After the age of twenty years or later the relative chest girth of men shows frequently a tendency toward a late secondary increase. A similar condition seems to exist in male gorillas, since an old male Mountain Gorilla had according to Akeley (1923) a stature of sixty-seven and one half inches and a chest circumference of sixty-two inches. From these dimensions index 1 a is calculated as 91.9 which is far above the value for the adult female gorilla XVI and the juvenile male Mountain Gorilla XIV. Indeed, this widening of the chest, late in life, seems to be much more pronounced in gorilla than in man. The large apes and man have developed a broad and stout trunk of great proportionate bulk, which is far removed from the long and slender trunk of lower primates. Gorilla has reached a greater extreme in this respect than man, a difference which exists already in fetuses (See Chapter 4).

The relative width of the shoulders (i 2 & i 2a) shows in general a tendency to decrease with age. The proportions based upon pelvic breadth vary so markedly that no clear changes of age can be recognized in the few available figures. From a study of photographs and skeletons of adult gorillas the author would expect that the pelvic breadth of adult males is smaller than the shoulder breadth, resulting in a proportion (i 4a) considerably lower than the value of 106.1, found in the adult female. Such a sexual difference in adult gorillas would be analogous to that existing in regard to this proportion between adult man and woman.

The nipples of gorilla are situated near the axillæ but not as much so as, *e.g.*, in the orang-utan; their exact position on the trunk seems to vary, as in other primates, more in a horizontal than in a vertical direction. That the nipples lie higher up on the trunk in gorilla than in man is evident from the following comparison: i 8 amounts to 83 in an infantile gorilla but averages 76 in human infants. In fetal life, however, this distinction is not yet present, since the same index amounts to 83.7 in gorilla fetus II and reaches a maximum in human fetuses of corresponding development of 85.3 (See Table 8).

In all primates the umbilicus shifts to a relatively higher position on the trunk with advancing growth (Schultz, 1926 b). In gorilla this tendency prevails also during fetal and infantile life, but subsequently the index for this relative position (i 9) would undergo a marked drop in case the low values in the two adult gorillas can be relied upon. If any trace at all of an umbilical scar is left in adult apes, this is usually so faint and uncertain that erroneous determinations of its location can easily be made.<sup>14</sup> It seems advisable, therefore, to await further data on the relative position of the umbilicus in adult gorilla and to consider the present evidence as insufficient for concluding definitely that the umbilicus shifts downward late in growth.

The lower end of the trunk of gorilla fetus II shows several features which necessitate detailed discussion. The tip of the tail in this specimen has not yet disappeared, or, more specifically, has not yet become overgrown by neighboring tissue (See Pl. IV, fig. 2). This last remnant of an outer tail is called "coccygeal tubercle", corresponding to its German name "Steisshöcker". This appellation in its strictest sense perhaps may not be entirely justifiable, since the tip of the last coccygeal vertebra reaches only to the base of this tubercle. The form and location of this fetal structure leave no doubt that it corresponds to the end of the relatively much larger embryonic tail and, incidentally, not to the so-called caudal filament, which develops temporarily on the embryonic tail.<sup>15</sup> In man

<sup>14</sup> Ehlers (1881) himself states that he is not quite certain whether he located the umbilicus in his adult gorilla (XVII) correctly. The measurements by the same author on the position of the umbilicus in the gorilla infant VII must contain some very evident error, since, when figured with the writer's method, the height of the umbilicus (m. 8) is found to equal 101 mm., whereas the height of the trunk (m. 4) amounts to 170 mm. These values combine in the impossible proportion (i 9) of 59.4, according to which the umbilicus would have been situated over the lower end of the sternum!

<sup>15</sup> It is most likely this caudal filament, and not the end of the true tail, which has persisted in those rare cases of "external tails" found among man and apes at stages of growth long after that, in which the last trace of a tail has normally disappeared from the surface. For instance, the minute pendulous appendage over the coccyx of a young chimpanzee, which has been pictured by Rosenberg (1876), resembles in every detail an undoubtedly persisting caudal filament, found and studied by the author in a human fetus of the fifth month (No. 730, Carnegie Laboratory of Embryology).



the coccygeal tubercle disappears normally in fetuses ranging in sitting height between 33 and 52 mm. (Kunitomo, 1918). In rare instances it may persist to the 60 mm. stage, but most frequently it is already missing in specimens of 40 mm. It is very surprising to find from the data collected in Table 3 that the stage of development, in which this tubercle disappears, is so greatly at variance in the

TABLE 3.

Fetuses and infants of the higher apes, for which definite information is available in regard to the presence or absence of the coccygeal tubercle. The vertex-coccyx curve is always considerably longer than the corresponding straight measurement on the same specimen. All measurements are given in millimeters.

Primate:	Number	Age	Vertex-coccyx (straight) or Sitting height:	Vertex-coccyx curve (with tape):	Observer:	Coccy- geal tubercle:
GIBBON	1	fetus	21.5	....	Schultz	<i>present</i>
	11	fetuses	56 to 173	....	Schultz	absent
	23	fetuses	....	62 to 222	Schwalbe, 1911	absent
	1	fetus	136	....	Schmidt, 1892	absent
ORANG-UTAN	1	fetus	....	56	Schwalbe, 1911	<i>present</i>
	1	fetus	....	75	Schwalbe, 1911	<i>present</i>
	1	fetus	....	115	Schwalbe, 1911	absent
	1	fetus	approx. 135	177	Schwalbe, 1911	<i>present</i>
	3	fetuses	145 to 230	....	Schultz	absent
	4	infants	264 to 317	....	Schultz	absent
CHIMPANZEE	1	fetus	185	.....	Bolk, 1926 b	<i>present</i>
	1	newborn	260	....	Schultz	absent
	1	infant	337	....	Schultz,	absent
GORILLA	1	fetus	88.5	....	Schultz	<i>present</i>
	1	fetus	135	....	Deniker, 1885	absent
	1	fetus	170	....	Bolk, 1926 b	absent

different apes. In the gibbon the coccygeal tubercle was well developed in a fetus of 21.5 mm. but in two specimens of respectively 56 and 62 mm. sitting height (one measured straight, the other one in a curve) no trace of this structure was remaining, and in 33 older fetuses the tubercle was also missing. In the gibbon, therefore, the tubercle disappears at an early stage of development, just as in man. In gorilla it persists considerably longer, *i.e.*, at least to the 88 mm. stage. In orang-utan it is found in a still larger fetus, though in another one (No. 3, Chapter 2) of the same size as gorilla fetus II it has already disappeared. Chimpanzee retains this structure longer than any of the other higher primates, since it is very conspicuous in a fetus with a sitting height of 185 mm. The author is unable to advance any plausible hypothesis to account for this wide discrepancy in the time of the final ontogenetic disappearance of the tail. One might be inclined at first to explain these embryological findings by the assumption that the phylogenetic degenera-

tion of the tail had occurred earlier in man and gibbon than in the three large apes. Such a possibility, however, is rendered highly improbable by the fact that the reduction of the tail has reached a greater extreme in adult orang-utan than in adult man (Wiedersheim, 1908; Schultz, 1926 a).

The female external genitalia of gorilla fetus II correspond fairly closely to those of a human fetus of the same stage of development (See Pl. IV, fig. 2). The groove on the lower side of the clitoris is very little developed in the gorilla. The labia majora of the latter are relatively smaller than in the human fetus, but they are rather high and hence clearly visible in a side view of this specimen (See Pl. I). Under the magnifying glass hair follicles can be recognized on the labia majora of the gorilla fetus, so there can be no doubt as to their identity. In Deniker's gorilla fetus III the labia majora are proportionately very much larger than in specimen II. They are also very well developed in the still older chimpanzee fetus, described by Bolk (1926 b). During postnatal life the labia majora undergo a marked reduction in the three large apes, indeed, many authors have claimed that they are entirely missing. Thus Bischoff (1879) and Gerhardt (1906) did not find these structures in gorilla, the former having studied three young specimens, the latter an adult. Deniker (1885), on the other hand, reached the conclusion from his material that the labia majora do not disappear completely in gorilla and in orang. Bischoff, likewise, observed a faint indication of these labia in the latter ape and Klaatsch (1892) found them in a juvenile orang. Friedenthal (1910), however, is of the opinion that the labia majora, observed by him in an orang, are not directly comparable to those in women. The same author denies their existence in chimpanzee, as does Bischoff, but a number of other authors, as *e.g.*, Symington (1889), Sperino (1897), and Sonntag (1923), have examined female chimpanzees which possessed rudimentary but undoubted labia majora. The conflicting reports on this point permit the conclusion that the degree of ontogenetic reduction of the labia majora varies a great deal in the anthropoids. It is certain that these structures are laid down in fetal life, but, whereas in man they persist throughout growth, in the anthropoids they undergo a process of atrophy, which in many cases leads sooner or later to their complete disappearance. It is very interesting to find that the gibbons and siamangs stand in this respect closer to man than do the three large apes, since the labia majora in the family *Hylobatidae* are not only well developed in the fetus, but are retained as comparatively large structures throughout postnatal growth, when the labia minora are

becoming smaller and gradually almost or entirely disappear from outside view (See Pl. IV, fig. 3.)<sup>16</sup>

This consideration of the conditions on the lower end of the trunk must include some remarks on the ischial callosities which are usually claimed to be totally absent in the anthropoid apes. Several authors have published independently and without referring to one another various observations which contradict the above mentioned claim. These observations will be quoted in the following and thus be brought together for the first time. Some brief remarks on the ontogenetic development of ischial callosities will be added in the hope that these combined notes may lead to a better understanding of the gradual evolutionary disappearance of these structures among the higher primates.

Friedenthal (1908 b) has given an illustration of well formed ischial callosities in an adult male orang-utan (*l.c.*, fig. 1, plate VIII) and one of small but well defined callosities in a young male chimpanzee (*l.c.*, fig. 7, plate III). In the same publication this author states: "Bei Schimpanse (Gorilla?) und Orang bilden sich im späteren Leben in Anpassung an das Sitzen auf den Sitzknorren schwache Gesässchwien aus, welche nicht wie beim Menschen durch die starke Gesässmuskulatur vor Druck geschützt werden, wenn auch niemals so auffällige hornige Schwien gebildet werden wie bei der Mehrzahl der Ostaffen." Lönnberg (1917) observed these callosities in chimpanzee and traces of them in gorilla. Speaking of *Gorilla beringei mikenensis* he says: "There are [in one adult female] no regular or distinct ischiadic callosities, but in the place of such there is a bare patch on either side, and the skin of these is, in counteraction to the rubbing and wearing, thickened and the horny layer has a tendency of peeling off in flakes. It may be said to be ischiadic callosities in being. In the old male there is no trace of such a bare place, but in the semi-adult male the hair is worn off on two symmetrically situated small spots in the ischiadic region corresponding to these patches in the female." Lönnberg's description of a series of ten chimpanzees (*Anthropopithecus cottoni*) from one locality contains the following comment: "All the adult specimens are provided with very well developed ischiadic callosities. These are largest in the old ones, f. i. 7 x 4 cm. in the old male; 6.5 x 3.5 cm. in the oldest female. The callosities are so thoroughly developed that they can be seen very plainly from the inner side of the skin as well. In the young animal with milk-dentition the

<sup>16</sup> Besides the specimens on Pl. IV, fig. 3 the author has examined several other female gibbon fetuses and two nearly adult female *Symphalangus syndactylus*, all of which agreed very well with the above findings. In the siamangs the labia majora were covered with many short, black hairs, whereas the gibbon of Pl. IV, fig. 3, had fewer but longer hairs on these places. Pocock (1925) mentions that in two adult female *Hyllobates lar*, examined by him, "there were a few hairs on the labia of the vulva."

callosities can hardly be more than traced on the skin." An infantile male chimpanzee of the National Museum (No. 154,183, species not determined, sitting height 461 mm.), kindly lent to the author by Mr. G. S. Miller, Jr., possesses fairly large and quite conspicuous ischial callosities. In a great many other chimpanzees and oranges, examined by the writer, there was absolutely no trace of true callosities, but it was noted that the length and density of the hair in the zones overlaying the ischial tuberosities vary a great deal, quite a few of these specimens being nearly bare on these places without, however, showing any thickening and hardening of the skin.

In gorilla fetus IV Bolk found the hair in the region, in which these callosities could be expected, to be arranged in the form of spirals. In the slightly older chimpanzee fetus of the same author these places were entirely free of hair. The writer agrees with Bolk's interpretation of these findings, which is quoted herewith: "Die Bedeutung der haarfreien Stelle am Perineum des Schimpansen darf vielleicht eine nãmliche sein als jene der beiden para-analen Spiralen beim Gorilla, eine Reminiszenz an die ebenfalls vœllig haarfreien Gesãssschwien niedriger Affen. . . . Bei menschlichen Embryonen lãsst die Haarrichtung keine Andeutung derselben sehen."

The ischial callosities of catarrhine monkeys make their appearance before the lanugo develops on the caudal end of the trunk, there is, therefore, never any hair on the place of these callosities. Among fetuses of *Colobus* monkeys, for instance, no lanugo is present as yet in a specimen with a sitting height of 89 mm. but the callosities are already clearly indicated by a more pronounced smoothness and slightly greater thickness of the skin in these places than in the surrounding region. In four older *Colobus* fetuses, ranging in sitting height from 112 to 147 mm., the lanugo has appeared but does not extend over the areas, occupied by the developing callosities.<sup>17</sup> In contrast to these conditions in lower primates the callosities of the gibbon develop late, *i.e.*, considerably after the lanugo has started to develop and not until after their typical place has been temporarily covered by very fine hair. This mode of development was studied by the author especially on the splendid gibbon material (*Hylobates pileatus*) which the late Dr. R. A. Spaeth had generously collected for the Anatomy Department of the Johns Hopkins University. A fetus of 102 mm. sitting height showed neither lanugo nor callosities. In the next older specimen, measuring 158 mm., very fine and extremely short hair is seen under magnification to extend uninterruptedly over

<sup>17</sup> Three of these *Colobus* fetuses have been described by the author in a special paper (1924 b); the remaining two, which belong to the collection of the U. S. National Museum, were studied more recently.

the gluteal regions, including the zones overlying the ischial tuberosities. A fetus of *Hylobates mülleri* (161 mm.) showed exactly the same conditions and the gibbon fetus (vertex – coccyx = 136 mm.), described by Schmidt (1892), must have reached a similar stage of development judging by the following statement by this author: “. . . wenn man die Gesässpartie genauer mit der Loupe prüft, so erkennt man, dass diese ganze Region, und insbesondere auch die Stellen, wo die Gesässschwienel sitzen würden, gleichmässig eine Anzahl feinsten Härchen, die nur Bruchteile eines Millimeters lang sind, trägt. Die Haut über den Sitzbeinknollen unterscheidet sich in nichts von der umgebenden Haut, und Callositäten an diesen Stellen lassen sich mit Sicherheit ausschliessen.” In a still older fetus of *Hylobates pileatus* (sitting height 169 mm.) there occurs the first indication of the ischial callosities in the form of two symmetrically placed hair-free zones, each about 3 mm. in diameter. The short hair surrounding these bare areas is directed toward their centers.<sup>18</sup> In the gibbon fetus of Deniker (1885), in which the hair was much more developed than in any of the above mentioned specimens, the bare ischial areas are considerably larger than in the oldest *H. pileatus* fetus, but not yet as large as in an infant of the same species, measuring 198 mm., or as in a new-born *H. lar* with a sitting height of 173 mm. Only in the last two specimens have the ischial callosities become horny or really callous.<sup>19</sup> Even in the infant, however, the callosities have not yet attained as relatively large a development as in adult gibbons.

With this rather lengthy digression the following conclusions seem justified. The ischial callosities are most strongly developed in the catarrhine monkeys, appearing very early in their ontogeny. In the gibbons they develop very much later, actually replacing a primary coat of hair. In the large apes they can occur in occasional specimens (in chimpanzee perhaps as a specific character?), the least tendency in this direction existing in gorilla, in which callosities are at best indicated by mere traces. That these callosities, when present in the apes, may become accentuated with advancing age through pressure and friction is not at all impossible. However, that these occasional callosities can not have been caused merely by mechanical action, as Friedenthal is inclined to believe, is evident at least from the

<sup>18</sup> The direction of the hair in this region may apparently vary, since Schwalbe (1911), in speaking of a gibbon fetus of 218 mm. vertex-coccyx length (measured with tape), makes the following remark: “Die kranio-kaudal gerichtete Behaarung des Rückens setzt sich in derselben Richtung neben dem After und den nur angedeuteten Gesässschwienel auf das Glutealgebiet fort.”

<sup>19</sup> In the lower monkeys the thickening and subsequent hardening of the skin over the ischial tuberosities begins at a relatively much earlier stage of development. For instance, in two *Pithecus rhesus* fetuses of the author's collection (sitting heights 163 and 167 mm.) these callosities are already modified into horny layers. An enlarged reproduction of a section through the thick callosity of a baboon fetus can be seen in a publication by Anthony and Villemin (1923).

occurrence of hair-free zones over the ischial tuberosities in the prenatal life of chimpanzee, a condition which is identical with the first stage in the development of these callosities in the gibbon.

#### Chapter 9. LIMBS.

All the proportions pertaining to the extremities of gorilla are collected in Table 4. In relation to the height of the trunk the length of the limbs changes comparatively little in the course of growth, at least as far as can be judged by the variable indices 10, 19, and 19a. Fetus III has the relatively longest limbs of the entire series, or rather the relatively shortest trunk. Disregarding this fetus, which in these proportions represents most likely an extreme variation, it appears that the relative length of the upper limb increases in general from early fetal to late infantile life, but reverses the trend of its growth thereafter to a slight secondary decrease. Expressed in figures this proportion (i 10) rises from 160 in fetus I to 191 in infant XII, but drops from there to 156 in the adult XVII. This constitutes a new confirmation of the following statement, made by the author in 1924 (a): The relative length of the upper extremity shows an initial increase in all primates, reaching its maximum at varying stages of growth and followed by a subsequent decrease which, however, in some forms, such as man, may change still later into a second rise. That the maximum in this relative measurement is attained before, and is also greater than in adult life, is shown by the following additional examples: Total length of upper limb in percentage of trunk height (i 10) in orang-utan: fetus (145 mm. sitting height) 195.5, infant 280.5, adult (7) 207.2; gibbon: fetus (4) 181.5, infant *H. pileatus* 219.0, infant *H. lar* 237.2, adult *H. leuciscus* 219.0, adult *H. lar* 230.8, adult *H. agilis* 232.3, adult *H. concolor* (8) 280.0; rhesus monkey: fetus (close to term) 167.6, adult 124.9; baboon: fetus (116 mm. sitting height) 129.0, new-born (225 mm. sitting height) 170.1, adult 140.0. The length of the lower extremity, whether including the height of the foot or not (i 19 & i 19a), shows a slight tendency to increase with advancing growth in its relation to the trunk height.

The proportion between the length of the upper and that of the lower limb (i 26 & i 27) is rather variable, but in spite of this, these indices show in general a slight decrease in the course of development, indicating that the lower extremity grows somewhat more intensely than does the upper one. If the total limb lengths are considered (i 26) the upper one amounts to more than 150 per cent of the lower one in the fetuses and infant, but to only about 140 per cent in the juvenile and adults. The intermembral index (i 27) formed only of the proximal and middle

limb segments is very high in the first and third fetuses, but very low in the second and fourth. The fact that fetuses I and II differ so much in the latter proportion, but so little in the former, can be traced directly to the difference in the relative length of the hand between the two fetuses, since the hand amounts to only 24.6 per cent of the total length of the limb (i 14) in fetus I but to 30.2 per cent in fetus II. The decrease of index 27 during postnatal life is best demonstrated on the average values derived from the exact and reliable measurements on skeletons. They amount in the infants (XI) to 123.7, in the juveniles (XV) to 118.6, and in the adults (XVIII) to 117.1 (See also Table 5). It may be mentioned here that an ontogenetic decrease in this proportion forms the rule in primates, but, whereas in most monkeys and apes the decrease is not very marked, it is very great in man. While discussing this particular index attention is called to its apparent tendency to differ in at least two of the species of gorilla. This difference is demonstrated in text-figure 1, and can also be seen in Table 5. The sum of the humerus and

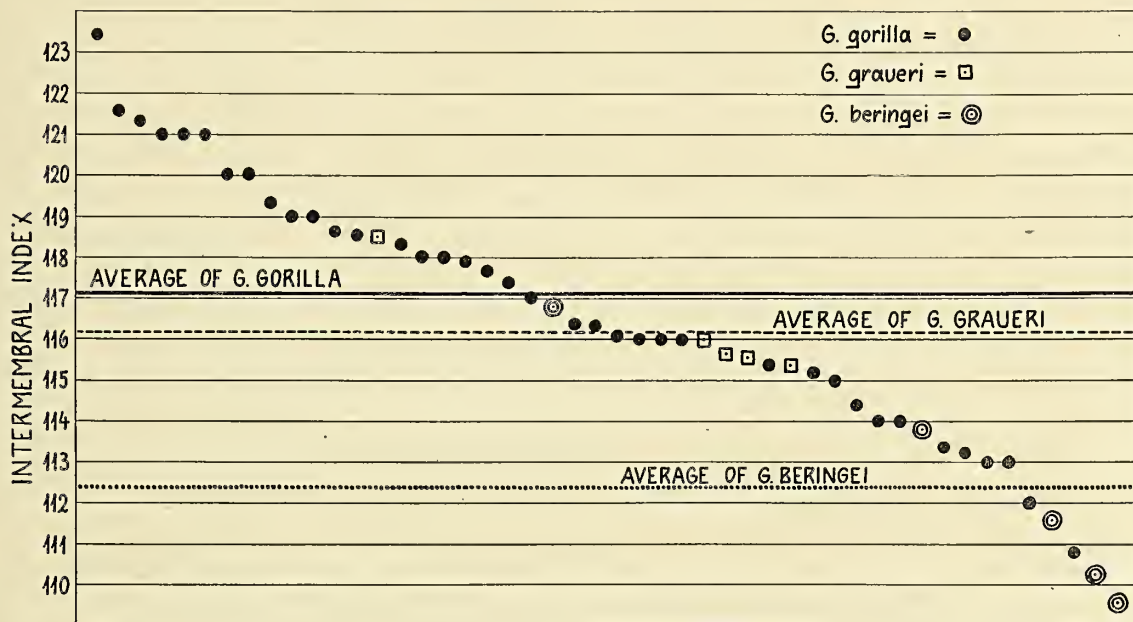


Fig. 1. Individual variations of the intermembral index (length of humerus+radius in percentage of length of femur+tibia) of thirty-eight adults of *Gorilla gorilla*, five adults of *G. graueri*, and five adults of *G. beringei*, grouped according to size of index. All these specimens are listed in Table 5.

radius lengths in percentage of the added lengths of femur and tibia averages in adult Lowland Gorillas 117.1 (with no noteworthy sex difference) and in the Highland Gorillas, (*Gorilla beringei*) 112.4. All the individual values of the latter fall below the average of the former, but the ranges of variation in the two groups overlap to a considerable extent. It can be said, therefore, that, whereas there exists no constant specific difference in this respect, *Gorilla beringei* shows never-

theless a clear trend toward having relatively shorter arms, or rather relatively longer legs, than *Gorilla gorilla*. The latter in this respect is removed somewhat further from man than is the former. In the author's opinion this distinction can be interpreted as indicating a greater adaptation to terrestrial life in the East African *Gorilla beringei* than in the West African forms. As will be pointed out later on, a study of the hands and feet in these two types of gorilla leads to corroborative conclusions. *Gorilla graueri* stands in regard to its intermembral index between *Gorilla gorilla* and *Gorilla beringei*, but, though a Mountain Gorilla, its average approaches that of the former more closely than it does that of the latter.

TABLE 4.  
Growth changes in the proportions of the limbs of gorilla.

Index No.	Percentage relation between:	Fetus I	Fetus II	Fetus III	Fetus IV	Infant VII	Infant VIII	Infant IX	Infant XI	Infant XII	Juven. XIII	Juven. XIV	Juven. XV	Adult XVI	Adult XVII	Adult XVIII
10.	Total upper limb l. (m.22) & Trunk h. (m.4).....	160.5	163.2	234.0	.....	177.6	186.0	.....	.....	191.0	.....	166.7	.....	176.0	156.0	.....
12.	Upper arm l. (m.23) & Total upper limb l. (m.22).....	39.6	37.7	38.4	.....	37.7	37.8	37.8	.....	39.7	.....	42.7	.....	39.0	40.6	.....
13.	Forearm l. (m.24) & Total upper limb l. (m.22).....	35.8	32.1	34.1	.....	33.8	31.6	35.8	.....	32.6	.....	32.1	.....	35.4	33.6	.....
14.	Hand l. (m.25) & Total upper limb l. (m.22).....	24.6	30.2	27.5	.....	28.5	30.6	26.4	.....	27.7	27.1	25.2	.....	25.6	25.8	.....
15.	Forearm l. (m.24) & Upper arm l. (m.23).....	90.5	85.2	82.2	92.6	89.5	84.0	94.5	83.8	82.0	.....	75.2	81.2	90.9	82.9	80.8
16.	Hand l. (m.25) & Forearm l. (m.24).....	68.4	93.9	80.9	.....	84.3	97.0	73.7	.....	85.0	.....	78.6	.....	72.0	76.5	.....
17.	Thumb l. (m.26) & Hand l. (m.25).....	.....	48.0	.....	.....	.....	.....	.....	.....	.....	.....	60.6	.....	42.7	.....	.....
18.	Hand b'dth (m.27) & Hand l. (m.25).....	.....	39.0	.....	.....	.....	.....	.....	.....	.....	.....	46.7	.....	36.6	.....	.....
19.	Total lower limb l. (m.15) & Trunk h. (m.4).....	103.0	107.9	.....	.....	115.3	.....	.....	.....	.....	.....	119.2	.....	126.2	110.8	.....
19a.	Thigh l. + leg l. (m.16 + 18) & Trunk h. (m.4).....	91.0	99.5	138.8	.....	.....	111.0	.....	.....	115.0	.....	108.4	.....	118.6	100.0	.....
21.	Leg l. (m.18) & Thigh l. (m.16).....	76.5	78.8	79.5	70.4	.....	83.0	96.2	83.1	83.0	.....	75.2	81.5	82.7	88.4	80.2
22.	Foot l. (m.19) & Leg l. (m.18).....	115.3	106.7	133.2	.....	.....	116.0	107.8	.....	112.0	98.5	107.1	.....	100.0	97.6	.....
23a.	Foot l. (m.19) & Vertex-coccyx l. (m.1 a).....	21.1	22.1	32.6	.....	34.7	.....	33.8	.....	.....	.....	30.3	.....	.....	35.0	.....
24.	Foot b'dth (m.21) & Foot l. (m.19).....	46.7	31.6	29.6	.....	.....	.....	34.3	.....	.....	.....	31.4	.....	.....	.....	.....
26.	Total upper limb l. (m.22) & Total lower limb l. (m.15).....	155.8	151.2	.....	.....	154.0	.....	.....	.....	.....	.....	139.6	.....	139.5	140.7	.....
27.	Upper arm + forearm (m.23+24) & Thigh + leg (m.16 + 18).....	133.3	114.5	123.3	113.0	125.5	121.0	123.8	123.7	116.0	111.6	115.0	118.6	110.4	115.8	117.1
28.	Upper arm l. (m.23) & Thigh l. (m.16).....	123.4	110.6	121.5	100.0	.....	115.0	125.0	123.2	120.0	.....	114.9	118.9	105.7	119.2	116.7
29.	Forearm l. (m.24) & Leg l. (m.18).....	146.1	119.6	125.6	131.5	.....	118.0	122.8	124.3	119.0	.....	115.0	118.5	116.2	111.9	117.5
30.	Hand l. (m.25) & Foot l. (m.19).....	86.7	105.2	86.4	.....	80.3	96.0	84.0	.....	91.4	83.4	84.3	.....	83.7	80.4	.....

Of the three segments of the upper limb the upper arm is the longest and the hand the shortest at all stages of growth. The percentage participation of the lengths of upper arm, forearm, and hand in the formation of the total limb length shows no noteworthy and clear change with advancing growth, except that the relative hand-length has somewhat higher values among fetuses and infants than in the adults. (See i 12, i 13, and i 14 in Table 4). Attention must here be called to the interesting fact that the segments of the upper limb have practically the



same proportionate lengths in adult gorilla as in adult man. Adult chimpanzee, orang-utan, and gibbon constitute a quite different group in this respect, since they have relatively shorter upper arms and relatively longer hands than the former two primates. As shown by Table 8, the upper arm amounts to 41 per cent of the total upper limb length in adult gorilla and in man, but to only 35 to 36 per cent in the other higher primates and the hand forms about 25.5 per cent of the total limb length in the former two, but 28.4 to 29.5 per cent in chimpanzee, orang, and gibbon.

TABLE 5.

Proportions between the long bones of the limbs of gorilla skeletons. Infants = series XI, juveniles = series XV' adults (*G. gorilla*) = series XVIII in chapter on material. All these gorillas are West African Lowland Gorillas, belonging in all probability to the various subspecies of *G. gorilla* (see Elliot, 1913). *Gorilla graueri* and *Gorilla beringei* are Mountain Gorillas from Central and West Africa. The proportions (from left to right) correspond very closely to the following indices in Table 4: i 15, i 21, i 27, i 28, and i 29.

Species	Age	Sex	Collection or Author	Percentage Relation Between					
				Humerus length	Radius Humerus	Tibia Femur	Hum.+ Rad. Fem.+ Tib.	Humerus Femur	Radius Tibia
<i>G. gorilla</i>	infant	?	Bolk, L. 1926. . . . .	152	86.2	81.6	124.7	121.6	128.4
"	"	"	Deniker, J. 1885. . . . .	170	81.8	85.2	123.5	125.9	120.8
"	"	"	Western Reserve University. . . . .	181	83.5	82.5	122.9	122.2	123.8
"	Juvenile	"	Bolk, L. 1926. . . . .	240	86.7	77.7	117.3	111.6	124.5
"	"	"	Mollison, T. 1911. . . . .	266	79.0	82.0	120.0	122.0	118.0
"	"	"	Johns Hopkins University. . . . .	276	77.9	84.8	118.5	123.1	113.1
"	adult	♀	Western Reserve University. . . . .	344	84.7	78.7	120.0	116.1	124.8
"	"	"	Mollison, T. 1911. . . . .	353	81.0	84.0	116.0	119.0	113.0
"	"	"	Lorenz v. Liburnau, L. 1917. . . . .	354	79.4	80.5	118.0	118.7	117.0
"	"	"	Mollison, T. 1911. . . . .	356	80.0	80.0	121.0	122.0	122.0
"	"	"	Western Reserve University. . . . .	357	82.4	81.1	119.3	118.5	120.4
"	"	"	Johns Hopkins University. . . . .	357	78.2	82.3	116.3	118.9	112.8
"	"	"	U. S. National Museum. . . . .	357	79.3	78.7	118.3	118.5	119.3
"	"	"	Mollison, T. 1911. . . . .	359	83.0	80.0	121.0	119.0	123.0
"	"	"	Western Reserve University. . . . .	360	84.2	83.3	121.3	120.7	122.1
"	"	"	Dealer's Store, Berlin. . . . .	362	80.1	78.7	121.6	120.6	122.8
"	"	"	Mollison, T. 1911. . . . .	365	82.0	85.0	113.0	115.0	111.0
"	"	"	Deniker, J. 1885. . . . .	370	81.5	78.0	110.8	108.5	113.8
"	"	"	Mollison, T. 1911. . . . .	378	81.0	83.0	113.0	115.0	112.0
"	"	"	Bolk, L. 1926. . . . .	380	80.3	78.6	118.7	117.6	120.0
"	"	"	Mollison, T. 1911. . . . .	382	79.0	81.0	117.0	119.0	116.0
"	"	"	American Museum of Nat. Hist.. . . . .	403	77.4	78.1	114.0	114.4	113.4
AVERAGE OF ADULT FEMALES. . . . .				365	80.8	80.7	117.5	117.6	117.7
<i>G. gorilla</i>	adult	♂	U. S. National Museum. . . . .	403	77.9	78.3	114.4	114.7	114.1
"	"	"	Mollison, T. 1911. . . . .	403	79.0	78.0	119.0	116.0	118.0
"	"	"	American Museum of Nat. Hist.. . . . .	407	81.6	80.6	118.6	117.9	119.4
"	"	"	Mollison, T. 1911. . . . .	412	78.0	79.0	116.0	117.0	115.0
"	"	"	American Museum of Nat. Hist.. . . . .	421	80.3	79.7	117.7	117.2	118.1
"	"	"	Johns Hopkins University. . . . .	424	78.9	79.5	115.4	115.8	115.0
"	"	"	Mollison, T. 1911. . . . .	424	79.0	78.0	120.0	118.0	121.0
"	"	"	Western Reserve University. . . . .	425	85.2	77.3	117.3	112.3	123.8
"	"	"	Lorenz v. Liburnau, L. 1917. . . . .	427	83.4	82.3	113.3	112.6	114.0
"	"	"	Mollison, T. 1911. . . . .	427	83.0	77.0	112.0	109.0	116.0
"	"	"	Mollison, T. 1911. . . . .	428	80.0	79.0	118.0	118.0	119.0
"	"	"	Mollison, T. 1911. . . . .	428	83.0	78.0	121.0	117.0	125.0

Species	Age	Sex	Collection or Author	Humerus length	Percentage Relation Between				
					Radius Humerus	Tibia Femur	Hum.+Rad. Fem.+Tib.	Humerus Femur	Radius Tibia
<i>G. Gorilla</i>	adult	♂	Columbia University . . . . .	432	80.5	80.5	115.2	115.1	115.1
"	"	"	U. S. National Museum . . . . .	433	81.3	78.3	117.9	116.0	120.4
"	"	"	Mollison, T. 1911 . . . . .	434	83.0	84.0	114.0	114.0	113.0
"	"	"	Mollison, T. 1911 . . . . .	435	85.0	77.0	119.0	115.0	126.0
"	"	"	Mollison, T. 1911 . . . . .	437	82.0	81.0	115.0	114.0	116.0
"	"	"	Lorenz v. Liburnau, L. 1917 . . . . .	440	80.0	85.8	116.1	119.8	111.7
"	"	"	Mollison, T. 1911 . . . . .	441	81.0	79.0	116.0	115.0	117.0
"	"	"	Bolk, L. 1926 . . . . .	452	83.6	80.1	113.2	111.0	115.8
"	"	"	Du Chaillu, P. B. 1861 . . . . .	457	75.7	80.0	123.4	126.5	119.6
"	"	"	Western Reserve University . . . . .	460	75.7	83.1	116.3	121.3	110.4
AVERAGE OF ADULT MALES . . . . .				430	80.8	79.8	116.8	116.1	117.4
AVERAGE OF ADULT MALES AND FEMALES ( <i>G. gorilla</i> ) . . . . .				402	80.8	80.2	117.1	116.7	117.5
<i>G. graueri</i>	adult	♀	Lorenz v. Liburnau, L. 1917 . . . . .	372	75.5	77.8	116.0	117.6	114.2
"	"	"	Lorenz v. Liburnau, L. 1917 . . . . .	385	74.5	76.0	115.6	116.6	114.3
"	"	♂	Lorenz v. Liburnau, L. 1917 . . . . .	428	79.2	77.0	118.5	117.2	120.5
"	"	"	Lorenz v. Liburnau, L. 1917 . . . . .	447	76.3	78.5	115.4	117.0	113.6
"	"	"	Lorenz v. Liburnau, L. 1917 . . . . .	465	75.5	80.7	115.7	119.2	111.3
AVERAGE OF ADULT MALES AND FEMALES ( <i>G. graueri</i> ) . . . . .				419	76.2	78.0	116.2	117.5	114.8
<i>G. beringei</i>	adult	♀	American Museum of Nat. Hist. . . . .	344	85.0	79.8	113.8	110.5	117.7
"	"	"	American Museum of Nat. Hist. . . . .	362	83.5	85.9	109.6	111.0	107.8
"	"	♂	American Museum of Nat. Hist. . . . .	390	88.5	79.3	110.2	104.7	116.8
"	"	"	American Museum of Nat. Hist. . . . .	412	87.4	83.1	111.6	108.9	114.6
"	"	"	U. S. National Museum . . . . .	435	83.2	79.5	116.8	114.4	119.8
AVERAGE OF ADULT MALES AND FEMALES ( <i>G. beringei</i> ) . . . . .				389	85.5	81.5	112.4	109.9	115.3

It is almost impossible to recognize a definite growth change in the proportion between forearm and upper arm (i 15) since the values for this index vary individually to a very marked extent. In general it may be said that this proportion shows a slight tendency to decrease with advancing growth. The forearm length of the small series of fetuses fluctuates between 82.2 and 92.6 per cent of the upper arm length, a range which is even surpassed by that of the adults (58 specimens) among which the radius-humerus proportion varies according to Tables 5 and 6 between 74.5 and 88.5. The latter range reaches far into the field of human variations since in individual cases the humero-radial index of adult man may be as high as 85.1, a value found by Sarasin (1916-1922) in a male Loyalty Islander, or reach an extreme of 87.6, obtained by the writer on the skeleton of an adult American negress. Fick (1926) has recently published the humero-radial index of ten adult gorillas, of which, however, he gives neither species nor sex. Judging by the length of the humerus, the majority of these specimens must be male. This series is listed separately in Table 6. If all the material of adult gorilla skeletons in Tables 5 and 6 is combined, an average humerus-radius proportion in these 58 specimens is obtained as 80.69 with a probable error of  $\pm 0.26$ . According to Martin (1914) the averages of this proportion range among human races from

71.3 to 81.5 and the average of the values for the 63 groups, listed by this author, amounts to 76.74. Man is characterized by having on an average the relatively shortest forearm of all primates (Mollison, 1911; Schultz, 1924 a & 1926 b), but gorilla, in this respect, ranks a close second. It may be mentioned also that, as there are marked racial differences in this proportion in man, so there are apparently differences between the species of gorilla, since *Gorilla graueri* has an average humero-radial index of 76.2, *Gorilla gorilla* one of 80.8, and *Gorilla beringei* one of 85.5. The difference between the first and the last mentioned form is indeed very striking, and particularly significant, since the ranges of variation do not overlap. On the basis of these figures it can be stated that at least one form of gorilla (*G. graueri*) has on an average as relatively short a forearm (76.2 per cent of upper arm length) as the average man (76.7 per cent of upper arm length). Chimpanzee, orang-utan, and gibbon, on the other hand, are far removed from man in this respect, since their forearms approach or even surpass their upper arms in length.

TABLE 6.

Radius length in percentage of humerus length in ten adult gorillas, according to Fick (1926).

Humerus lengths	Radius in pr. ct. of Humerus
352 mm.	80.7
387 "	79.3
420 "	81.9
420 "	83.3
445 "	80.9
445 "	81.1
460 "	78.3
460 "	77.2
469 "	78.9
478 "	79.1
Average	80.1

The percentage relation between leg length and thigh length (i 21) falls below 80 in the fetuses, but above that value in postnatal life, with the exception of the juvenile XIV. If the scanty and variable data for this proportion permit any conclusion at all, it can be stated in a preliminary way, that in general the leg seems to exceed the thigh in rate of growth, a condition which conforms with that prevailing in most primates, including man.

At several places above reference was made to the marked individual variations in body proportions of gorilla. The figures of Table 5 furnish an opportunity to add here some further comment on the variability of this ape. In the thirty-eight skeletons of adult *Gorilla gorilla* the humero-radial index ranged from 75.7 to 85.2, the femoro-tibial index from 77.0 to 85.8, the intermembral index from

110.8 to 123.4, the humero-femoral index from 108.5 to 126.5, and the radio-tibial index from 110.4 to 126.0. These wide ranges all indicate a variability which is at least equal to, if not at times larger than the variability of the same proportions in man. Sir Arthur Keith (1926) has recently stated that gorilla varies individually more than does man. Although the writer is not prepared to endorse this view unconditionally, he is convinced that gorilla is at least fully as variable as man.<sup>20</sup> This last conclusion is justified in regard to the limb proportions and is undoubtedly true also in regard to the skull of gorilla, as was shown for instance by the studies of Selenka (1899), Duckworth (1904 b), Bolk (1925), and Harris (1926).

*The hand and the foot.* The last part of this chapter will be devoted to the consideration of the distal segments of the limbs, the hand, and the foot. In only one (fetus II) of the specimens listed in Table 4 does the hand exceed the foot in length (i 30). Other indices in this table permit a more exact analysis of this exception, since it can be shown that it is not so much the foot which is unusually short (i 22 & i 23a), but that it is the hand which has a greater relative length (i 14 & i 16) than in any of the other gorilla fetuses. The percentage relation between hand and foot lengths of fetus II, amounting to 105.2, represents, therefore, in all likelihood not a typical step in the growth changes of this proportion but a rare variation. In the younger as well as in the older fetus (I & III) this index is much lower, namely 86.7 and 86.4. In all adults the hand is shorter than the foot in gorilla just as in the majority of other primates and particularly in man. A reversed relation exists chiefly in the gibbons, but also in some chimpanzees.

Fick (1926) has already pointed out that the hand of adult gorilla is unusually short in relation to the length of the upper limb (without hand). According to this author the hand length in percentage of the added humerus and radius lengths amounts to 31.7 and 33.2 in two adult gorillas, whereas in sixty-two human adults it averages 33.7, in two adult orangs 35.4, and in three adult chimpanzees 43.5. The writer's results agree very closely with these findings of Fick, since the same proportion (but taken on the outer body, instead of on the skeleton) was found to average 34.1 in 24 adult white men (series 5), and to be 34.4 in gorilla XVI and

<sup>20</sup> It must be borne in mind that our knowledge of the variability of a species depends to a great extent upon the number of specimens examined. Naturally, much larger series are available for the study of variability in man than for that in gorilla; so it is all the more surprising that even the comparatively scanty material of the latter reveals so wide a range of variation.

For the humerus-radius proportion of the combined series of fifty-eight adult gorillas, listed in tables 5 and 6, the standard deviation and its probable error amount to  $2.93 \pm 0.19$  and the variation coefficient to  $3.64 \pm 0.23$ . The degree of variability, indicated by these figures, becomes apparent from a comparison of them with the values of these coefficients for the very similar upper arm-forearm index of 100 adult whites, as given by Mollison (1911): Standard deviation  $2.79 \pm 0.13$ , variation coefficient  $3.56 \pm 0.17$ .

34.7 in gorilla XVII, 39.6 in an adult orang (7), 39.9 in an adult gibbon (8), and 41.8 in an adult chimpanzee (6) (See also i 14, Table 8). In young gorillas this relatively short hand length is as a rule not yet so pronounced. For instance, it amounted to 37.0 in one juvenile (Fick). This is furthermore demonstrated by the fact that the indices 14 and 16 in Table 4 show higher values among fetuses and infants than in adults. There can be no doubt that a relatively long hand is an arboreal character and hence typically simian, whereas a short hand is decidedly non-arboreal and much better adapted to a terrestrial mode of life. It is particularly interesting and suggestive, therefore, to find that gorilla has a non-arboreal hand length and that this condition becomes most pronounced during late ontogenetic development.

In all primates studied so far the embryonic hand is proportionately broad and the hand width decreases in relation to the total hand length during at least some periods of growth (Schultz, 1926 b). As shown on Pl. V the hand of gorilla is already quite slender in fetal life, but, curiously enough, it changes in later growth into a much broader shape. A cast of the hand of the three-year-old female gorilla, "Dinah", kindly lent to the author by Prof. McGregor, has a much slenderer form than the hands of the two adult gorillas, shown on Pl. V.<sup>21</sup> Relatively even broader than the last two is the hand of an adult male Mountain Gorilla, pictured by Akeley (1923). The statement of Du Chaillu (1861) that "the hand of the gorilla is almost as wide as it is long" must have reference to the palm alone, and not to the entire hand including the digits, but shows also that in adult gorillas the hand has become very broad; indeed, fully as much so as in man, and much more so than in any of the other primates. It is very significant that among monkeys the relatively broadest hand is found in the largely terrestrial baboons (Schultz, 1924 a).

The thumb of all the primates, previously studied by the author (1926 b), becomes relatively shorter with advancing growth, and man at all ages retains a proportionately longer thumb than do monkeys and apes. In extremely arboreal primates the thumb is short or even tends to disappear entirely. In gorilla the thumb is unquestionably relatively shorter and also relatively thinner in fetuses than in adults (See Pl. V, and also Pl. II, fig 1). In the former the thumb reaches not quite to the base of the index finger, whereas in the latter it reaches easily to that place or even as far as the distal third of the basal phalanx of the second

<sup>21</sup> The length-breadth proportion of the hand (i 18) of Lowland Gorillas amounts to 39.0 in fetus II, to approximately 35.0 in the three year old "Dinah", to 36.6 in the adult female XVI, and to 49.5 in the adult of Hartmann, but in Highland Gorillas to 46.7 in the juvenile XIV, to approximately 60 in the adult female, shown on Plate V, and to roughly 64 in the adult male of Akeley. Judging by these meagre data *Gorilla beringei* has a relatively broader hand than has *Gorilla gorilla*, and one even broader than have most human beings.

finger. In the Mountain Gorilla the thumb seems to have a greater relative length than in the Lowland Gorilla, judging by the fact that the young *Gorilla beringei*, XIV, has an index (17) of 60.6 and the adult *Gorilla gorilla* XVI one of only 42.7. This seems furthermore evident from a comparison of the two adult hands on Pl. V. In chimpanzee and orang the thumb is much weaker and reaches as a rule not as far as in gorilla. It is, therefore, again the latter ape which stands closest to man in the relative size of the thumb.

It must be mentioned also that the degree of rotation, *i.e.*, of opposability, of the thumb, varies a great deal in gorilla. As shown on Pl. V, the transverse axis of the thumb (determined by the nail) stands nearly parallel to that of the other digits in fetus II and the adult of Hartmann, but is rotated very considerably in fetus III and the adult of Akeley, the nail being plainly visible from the palmar side of the hand in the latter two, in which the thumb appears to be as opposable as in adult man.

These notes on the thumb and on the relative hand width tend to strengthen still further the argument advanced in connection with the above discussion of the relative hand length. It can all be summarized in the statement that gorilla possesses a relatively short and very broad hand with a proportionately strong and long thumb, all characters which are decidedly less arboreal than in the other apes and in which gorilla closely approaches, equals, or even surpasses man. The fact that the fetal and infantile hands are in all these points more simian than the adult hand suggests strongly the possibility that gorilla has become less adapted for arboreal life only in comparatively recent stages of its evolution. It is particularly interesting that this apparent emancipation from tree-life, if one may conclude from the conditions of the hand, seems to have advanced further in the Mountain Gorilla than in the lowland forms.

To this discussion on the hand of gorilla may be added some notes and quotations appertaining to a very interesting peculiarity in the knuckles of the African anthropoids. This seems particularly desirable since these scattered observations have never before been collected. Du Chaillu (1861), in speaking of the gorilla, states: "The skin on the back of the fingers, near the middle phalanx, is callous and very thick, which shows that the most usual mode of progression of the animal is on all-fours, and resting on the knuckles." The same can be said in regard to chimpanzees, which also support themselves on their flexed fingers, particularly on the middle phalanges, whereby most pressure is exerted on the joint between the basal and middle digital segments. Neither gorilla nor chimpanzee has any hair on the middle portions of its fingers, whereas the gibbon, for instance,

which does not use its knuckles in walking, does have hair on these places. The following rather unexpected findings on fetuses of African apes are especially significant in this connection. Referring to gorilla fetus IV Bolk (1926 b) mentions: "Was die Finger betrifft, war der Daumen auch bei diesem Embryo noch ganz unbehaart, von den übrigen Fingern war der Grundphalanx behaart wie beim Schimpansen, und überdies fanden sich auf den Endphalangen fünf bis sechs etwas straffe Härchen, die beim Schimpansen fehlten. Die eigentümliche Erscheinung, dass Grund- und Endphalanx wohl, Mittelphalanx dagegen nicht behaart ist, darf vielleicht erklärt werden durch die Tatsache, dass die Haut der proximalen Hälfte der Mittelphalangen ein wenig polsterartig hervorsprang infolge einer kräftigen Entwicklung der Epidermis. Die Oberfläche des Überganges von Mittel- in Grundphalanx schien wie mit kleinen Schwielenhöckern besetzt. Beim Schimpansen vermisste ich diese Bildungen." Though Bolk's chimpanzee fetus did not possess these "phalangeal callosities", they can occur in this ape at prenatal stages, as was shown by Friedenthal (1908 a), who made the following observation on a chimpanzee fetus, which is not as far advanced in development as Bolk's specimen: "Als auffälligen Befund zeigte der untersuchte Fötus des Tschego bereits haarlose Schwielen an den Fingern trotz Behaarung des Nagelgliedes der Finger. Die durch das Laufen auf den umgeschlagenen Fingern erworbenen Schwielen der anthropoiden Affen sind daher durch Vererbung in der gleichen Weise fixiert wie die Liegeschwielen der Kamele."

There can be no doubt that, connected with their special mode of walking, gorilla and chimpanzee have lost the hair on the middle phalanges of their fingers, show a thickening of the skin on these places with a tendency to its becoming callous, and that these peculiarities are at least in some instances present before birth. This, as was pointed out by Friedenthal, is directly comparable to the early ontogenetic appearance of certain callosities in camels. Further very similar conditions are found in the warthogs (*Phacochærus æthiopicus*) which are in the habit of kneeling on their carpal joints and thus sliding around while digging for roots. The places on which they kneel are protected by thick callosities, which already develop during fetal life (Weber, 1904, and others). The author is not concerned here with the question whether these conditions can be used as support for the theory of inheritance of acquired characters or whether they should be regarded as "favorable mutations", or, possibly, receive a still different interpretation.<sup>22</sup> Whatever explanation one may favor, one must bear in mind that the

<sup>22</sup> It may be mentioned here that according to Lowe (1926) the "sternal callosities" of the ostriches, which are present in the embryo and which differ histologically from true callosities, are reptilian-derived characters and can not be considered as inherited acquired characters.

callosities, discussed above, are of the same nature, though not nearly as strongly developed, as the ischial callosities. Thomson (1907) after referring to the same observations on warthogs, which are mentioned above, concludes with the following statement: "This seems to some naturalists to be a satisfactory proof of the inheritance of an acquired character. It is to others simply an instance of an adaptive peculiarity of germinal origin wrought out by natural selection."

The interesting growth changes in the gorilla's foot are illustrated on Pl. VI. The length-breadth proportion of the foot decreases during early fetal life. This index (i 24, Table 4) amounts to 46.7 in the youngest known gorilla fetus,<sup>23</sup> but has dropped to 31.6 in fetus II and to 29.6 in fetus III. It is approximately the same as in the last fetus in the three year old female gorilla "Dinah" (according to a cast of its foot, kindly lent to the author by Prof. McGregor) and in the five year old male, shown on Pl. VI. In the juvenile Mountain Gorilla XIV this index amounts to 31.4 and is, therefore, also still about the same as in fetus II. As adult life is approached the foot of some gorillas may become extremely broad, as shown by the adult of Brehm on Pl. VI. That the relative breadth of the foot of adult gorilla is at least as great as that of man and greater than that of other apes is shown by the following values for the index 24: average in adult man (according to Table 8) 28.0, Akeley's cast of the foot of an adult Mountain Gorilla approximately 29.7, cast of the foot of an adult chimpanzee approximately 25.5, adult orang-utan 23.8, adult gibbon 21.6 (the last two values according to Table 8).

The relative length of the great toe, *i.e.*, the place on the second toe to which it will reach when adduced, varies in gorilla to such an extent that it is impossible to recognize any definite marked growth change in this condition. The distance from the heel to the tip of the great toe measures about 82 per cent of the total foot length in fetus I; in fetus II this proportion amounts to 89.0, if the hallux is adduced; in fetus III to about 87; in the three year old "Dinah" to approximately 74; in the three-and-a-half year old "John Daniel II" (measured alive by the author) to 83.8; in the five year old specimen of Pl. VI to about 82; and in the adult of Hartmann to about 85. The same proportion amounts to 93.8 in the juvenile Mountain Gorilla XIV, and to about 92 in the adult Mountain Gorilla of Akeley. It is very noteworthy that both the latter values are considerably higher than those of any of the above enumerated Lowland Gorillas. A corresponding difference in species is obtained from measurements taken of the skeleton of the foot, as demonstrated by the following figures kindly supplied to the author by Dr. W. L.

<sup>23</sup> The outline drawing by Duckworth of the foot of fetus I (copied exactly on Pl. VI) is evidently foreshortened in a transverse direction, since from this drawing one would obtain a much smaller relative foot breadth than that derived from the direct measurements by the same author.



Straus, Jr.: Distance from tuber calcanei to tip of hallux in percentage of greatest length of skeleton of foot in *Gorilla gorilla*, infant (sex unknown) 79.5, two adult males 78.9 and 83.3; in *Gorilla beringei*, infant male 87.6, adult male 90.7. If it now can be stated that the great toe reaches further in the Mountain Gorilla than in the West African forms, it does not imply that the phalangeal part of this toe is longer in the former than in the latter. From a comparison of the feet of the adults of Akeley and of Brehm on Pl. VI it seems much more likely that the free portion of the great toe is considerably shorter, and hence the metatarsal or tarsal portion relatively longer in *Gorilla beringei* than in *Gorilla gorilla*. In consequence of this relatively short free portion of the great toe in the Mountain Gorilla the cleft between the latter toe and the second toe is also proportionately short; indeed, it is of relatively shorter length than in some few human feet. For instance, the length of this cleft (distance *A1* or *A* to *B* on Pl. VI) in percentage of the total foot length (distance *A* to *C*) amounts to 22.0 in the adult Mountain Gorilla, to 22.5 in the negro fetus with the relatively longest toes, shown on the plate and to even 23.6 in one out of twenty-six adult white males, measured by the author. In *Gorilla gorilla* this cleft has at all stages of growth a considerably greater relative length, but not nearly as great as in orang-utans.

For an interpretation of these notes on the great toe of gorilla the author must repeat what he has stated in a previous paper (1926 b): Among adult monkeys the great toe branches from the sole at a varying but always considerable distance from the base of the second toe. Among adult anthropoid apes this feature differs least from the human condition in the Mountain Gorilla, and most in orang-utan, with a greater discrepancy between the latter two than between gorilla (particularly the East African form, but holding true also in regard to the West African forms) and man. There can be no question that the opposability of the great toe is greatly facilitated by its branching at a place which is removed from the second toe, so that, in the act of grasping, these two toes together with the intermediate medial edge of the sole form diagrammatically a U, rather than a V, as in man.

The lateral toes II to V are relatively short in the gorilla, when compared with the orang and gibbon, but in the West African gorilla relatively long in comparison with man. In many individual cases these two toes are united by webs of varying length (See *e.g.* the adult of Brehm on Pl. VI), as has been reported by a number of authors from Du Chaillu in 1861 to Straus in 1926. The transverse flexure folds on the foot have been carefully compared and marked by numbers on Pl. VI. The folds 1 and 2 are caused, or at least accentuated, by flexion in the metatarso-phalangeal joints, which are situated between these folds and, as a rule, slightly closer to fold 2 than to fold 1. The folds at 3 correspond fairly

accurately to the joints between the basal and middle phalanges. Of these crease-lines that marked 1 is in the gorilla sometimes missing (adult of Brehm) or only partly developed (adult of Akeley), whereas in man it is never present and line 2 is generally but faintly indicated or also missing. It is very interesting to find by means of these flexure-lines as landmarks that the sole of man has crept further distally along the lateral toes than in most gorillas. In the former the planta proper reaches in general all the way to line 3, though in individual cases it may not yet extend so extremely far on the second and third toes. In the majority of West African gorillas, on the other hand, the sole reaches only to line 2, as in fetuses I and II and in the adult of Brehm, or beyond that line but not to fold 3, as in fetus III and the adult of Hartmann. It is possible, but not very likely, that the portion of the "sole", which in the latter cases extends beyond line 2, should be regarded as webbing between toes. However, by comparing the adults of Brehm and of Hartmann it seems much more probable that the former represents a clear case of webbed toes, whereas the latter represents one with a distally extended sole. At any rate, there can be no doubt as to the nature of this condition in the adult Mountain Gorilla of Akeley. In this specimen the region between folds 2 and 3 appears so evenly padded, that it forms one continuous pillow-like structure, differing in no respect from the part between the creases 1 and 2. Here one certainly does not deal with any web formation, but with a true sole, which has migrated to the proximal end of the middle phalanges, just as in man. In consequence of this extreme forward extension of the sole, which has no parallel among other apes or monkeys, the lateral digits of the adult Mountain Gorilla are separated to an even lesser extent than in many human feet, such as for instance the foot of the negro fetus with maximum relative length of toe, shown on Pl. VI. These short free toes of gorilla, particularly *Gorilla beringei*, form a striking contrast to the exceedingly lengthened, over-developed toes II to V of the adult orang. As those of the latter are justly regarded as an ideal adaptation to arboreal life, so must the short toes of the former be interpreted as unsuitable for effective tree-climbing and as being more in accord with terrestrial habits.

The heel of gorilla is in most cases quite prominent, projecting beyond the profile of the ankle region. This condition may be very pronounced even in the fetus, as for instance in the specimen of Deniker, shown on Pl. II, fig. 2. Du Chaillu (1861) states that "the heel in the gorilla makes a more decided backward projection than in the chimpanzee." The relative degree of prominence of the heel was observed by the author as "very prominent" in two plaster casts of gorilla feet and in one live gorilla; "fairly prominent" in another cast of the foot of a gorilla; among ten preserved chimpanzees and one plaster cast of the foot of a chimpanzee as "fairly

prominent" in five cases, and as "not prominent" in the remaining six instances; among fourteen preserved orang-utans and one plaster cast of an orang foot as "very prominent" in one case, "fairly prominent" in four cases, and as "not prominent" in ten cases. Finally, it may be mentioned that in gibbons and monkeys the heel is never prominent, and that in man there exist marked racial differences in this respect (Schultz, 1926 b), since negroes possess a much more pronounced prominence than whites. While the gorilla equals man in regard to the prominence of its heel, it surpasses man in the relative width of the heel region of the sole. The juvenile and adult gorilla feet on Pl. VI show clearly that the sole of this ape does not become so narrow in the heel region as it does in the human foot, but is of nearly equal width underneath and behind the ankle as at the metatarsophalangeal joints. In gorilla fetuses this is not yet the case, since the region of the heel still tapers to a narrow, almost pointed shape.

The conclusions to be drawn from this discussion of the foot of the gorilla are very similar to those derived from the study of the hand. Like the hand, the foot is still more typically simian and arboreal in fetal stages of development than at the completion of growth. Fetus II supplies the best example of this. In this specimen the phalangeal portions of all the toes are relatively long, the great toe branches from the sole proportionately far from the base of the second toe, and the heel is narrow and rather pointed, all features characteristic of a climbing foot, though not developed to such extremes as in the orang and gibbon. The foot of the adult Mountain Gorilla seems to be built according to a quite different plan. Here the free digits are very short and can not possibly be as mobile as the long and slender fetal toes. The great toe is relatively thicker and stronger, reaching more distally than in the fetus, and branching from the sole further forward, *i.e.*, at flexure fold 2 instead of 1 as in the younger stages. Finally, the heel has become very broad in the adult, forming a huge pad, ideally adapted for supporting the enormous weight of the body while walking on the ground. Some of these features, chiefly the relative lengths of the toes, have not departed so much from the arboreal type in the adult Lowland Gorilla as in the adult *Gorilla beringei*.

Without knowing anything of its habits one might deduce from the conditions of the foot of adult *Gorilla beringei* that this ape, the heaviest of all primates, must at best be but poorly adapted for climbing in trees. Such a conclusion is fully borne out by the following statement of Akeley (1923), who has had such enviable opportunities to study the Mountain Gorilla in its native environment: "I believe that he has nearly passed out of the arboreal phase of life and is perhaps entering the upright phase and that he is the only animal, except man, that has

achieved this distinction. To stand erect and balanced, an animal needs heels. The plaster cast of the gorilla's foot . . . is evidence . . . that the gorilla has developed a heel." Later on Akeley adds: "The German, E. Reichenow, who observed gorillas in this same area, agrees that the gorilla is seldom in trees."

### Chapter 10. HEAD.

In all higher vertebrates the head becomes proportionately smaller with advancing growth. That the gorilla conforms to this rule is demonstrated by the indices 31 a and 33 a in Table 7. The average diameter of the head may, for instance, amount to nearly 90 per cent of the height of the trunk in a fetus, but to only 40 per cent in a juvenile. The side views of the heads of gorillas on Pl. VII show the decrease of the relative height of the head (ear opening to vertex) and the closely connected rapid lowering of the forehead with advance in growth. The gorilla fetuses I and II differ relatively little in regard to these points from the negro fetuses I and II, but in later stages of development the forehead of gorilla is much lower than the human forehead and the entire sagittal curvature of the brain-case has become flatter.<sup>24</sup> This is also evident from the growth change in index 34a.

TABLE 7.  
Growth changes in the proportions of the head of gorilla.

Index No.	Percentage relation between:	Fetus I	Fetus II	Fetus III	Fetus IV	Infant VII	Infant IX	Infant X	Juv. XIII	Juv. XIV	Adult XVII
31 a.	Horiz. head circumf. (m.34) & vertex-coccyx l. (m.1 a) . . . . .	123.8	120.0	128.1	....	....	95.1	....	....	....	....
33 a.	Average head diam. (m.28 a) & Trunk h. (m.4) . . . . .	80.3	80.2	89.8	....	....	....	....	....	40.3	....
34 a.	Head l. (m.30) & sagittal arc of head (m.35) . . . . .	....	56.6	....	....	....	....	....	77.8	....	....
35.	Head br. (m.32) & head l. (m.30) . . . . .	82.8	90.9	82.8	89.2	....	75.6	77.2	78.6	78.9	....
40.	Face br. (m.41) & head br. (m.32) . . . . .	91.7	86.2	102.0	....	....	92.3	....	100.0	98.5	....
43.	Nose br. (m.43) & face br. (m.41) . . . . .	34.1	45.0	38.8	....	....	42.3	....	....	....	....
44.	Nose br. (m.43) & Nose h. (m.42) . . . . .	93.7	133.3	95.1	....	....	78.9	....	....	....	....
45.	Interocular br. (m.44) & biocular br. (m.45) . . . . .	33.3	40.8	35.3	....	....	34.9	....	34.4	....	....
46.	Interocular br. (m.44) & face br. (m.41) . . . . .	27.3	28.4	24.5	....	....	22.7	....	20.0	....	....
47.	Mouth br. (m.46) & face br. (m.41) . . . . .	45.5	45.0	53.1	....	....	53.6	....	55.4	....	....
48.	Ear br. (m.48) & ear h. (m.47) . . . . .	58.4	67.8	62.5	....	....	64.3	....	71.1	....	62.7
49.	Ear h. × br. (m.47 × m.48) & Head l. × tot. h. (m.30 × m.38) . . . . .	2.3	4.7	4.6	....	....	6.0	....	8.2	....	....
49 a.	Ear h. (m.47) & total head h. (m.38) . . . . .	18.7	26.2	26.7	....	34.7	30.9	....	31.1	....	33.7

<sup>24</sup> Bolk (1926 b) compared the profile of the head of his gorilla fetus with that of a human fetus by superimposing one on the other, without regard to the skull base or the ear-eye horizon, these being situated much higher in the ape than in the human fetus. In this way he reached the following conclusions, which could not have been drawn, if the ear openings of the gorilla had been shifted down to the level of those of the human fetus: "Die starke Gehirnentwicklung [speaking of fetus IV] hat eine Ausbildung der Stirn zur Folge, welche gleich hoch als beim menschlichen Fetus gewölbt ist . . . Diese Superpositionszeichnung zeigt, dass die Schädelwölbung des Gorillafetus mit jener des Menschenfetus ziemlich genau übereinstimmt."

The length-breadth proportion of the head, or the so-called cephalic index (i 35), shows a clear tendency to decrease in general with advancing age, the values for fetal life being higher than those for any of the postnatal growth stages. The marked fluctuations of this index in the fetuses and its apparent slight increase after birth are in all likelihood explained by the great variability in the shape of the head of the gorilla, which ranges from dolichocephaly to brachycephaly, as has been shown by Oppenheim (1912), Bolk (1925), and Harris (1926). That the cephalic index is very high in fetuses of all the higher primates is proved by the following figures: Among many hundreds of human fetuses it averages 87.4 in the third month, decreasing to an average of 81.5 in the ninth month, and ranging individually to as much as 98.0 (Schultz, 1926 b); in gorilla it ranges from 82.8 to 90.9 (Table 7, i 35); in the chimpanzee it varies between 83.1 and 90.7 (the younger fetus of Friedenthal, 1914, has an index of 89.3, the older fetus one of 86.8, Bolk's fetus [1926 b] has the minimum value, and Anthony's fetus [1918] the maximum); in orang-utan variations extend from 78.9 to 95.0 (four fetuses described by Schwalbe [1914], and three fetuses measured by the author, the latter having values of 87.4, 91.7, and 92.1).

The occiput of the head of the gorilla seems to become slightly more prominent with advancing fetal development, since it does not project at all beyond the profile of the neck in fetus I, but is quite prominent in fetus IV. The degree of prominence in the latter specimen is greater than in any other gorilla; particularly in later stages of growth this prominence of the occiput becomes again very much less pronounced, disappearing entirely after infantile life. In man the occiput can be much more prominent than in gorilla fetus IV, at least after the middle of fetal development.

The nose of gorilla becomes in general narrower in relation to its height (i 44) with advancing growth (See Pl. IV, fig. 1 and Pl. VIII, Fig. 1). Fetus II has an extremely broad nose in proportion to nose-height as well as to the breadth of the face (i 43). In fetuses I and II the nasal septum is still very broad, almost as in platyrrhine monkeys, and the nostrils are relatively small. However, in the third known fetal stage of gorilla the septum has already narrowed to the thin partition typical of catarrhines, and the nostrils have become greatly enlarged. Soon after birth the nasal openings of gorilla develop to a proportionate size which exceeds that of any other primate (See Pl. IV, fig. 1 and Pl. VIII, fig. 1). The nose of the two youngest fetuses is, as shown clearly on Pl. VII, at least as prominent as in negro fetuses of corresponding development. The nasal bridge lies far in front of the eyes and there is a distinct nasal apex. In later growth

stages, however, nothing is left of the latter and the nasal bridge has sunk between the bulging eyes in fetuses III and IV. Nevertheless, the gorilla possesses throughout growth a more prominent nose than the other apes, and, indeed, one which is as much elevated as in some human beings. This is best demonstrated by a comparison between the horizontal sections through the nasal region of various higher primates given on Pl. VIII, fig. 2. The interorbital curve *a* of the siamang, orang, and chimpanzee is almost straight, indicating a flat nasal bridge, as in the chimpanzee shown on Pl. IV, fig. 1. The lower curve *b* shows that at their lower end the nasal bones of these apes also do not project forward, but can at times even form a concavity, as in the adult chimpanzee. Man and gorilla form a sharp contrast to these conditions. Section *a* as well as *b* of the juvenile and the adult gorilla are bent forward more strongly than in the flat-nosed negress, but not as much as in the white with an extremely prominent nose. All gorillas after infantile age have, as far as the author can ascertain, along the upper part of the nasal dorsum a median ridge (See Pl. IV, fig. 1) which shows clearly on the horizontal section *a* of the skull.

Just as the nasal aperture lies much further below the lower edge of the orbits in gorilla than in chimpanzee (Pl. VIII, fig. 2) so are the nasal wings further removed from the lower eyelids in the former than in the latter (Pl. IV, fig. 1). In consequence the upper lip of gorilla is much lower than that of chimpanzee or, incidentally, that of orang, differences which are present already in the older fetuses and infants (Pl. VIII, fig. 1). As in all primates, the interocular breadth of gorilla becomes smaller in relation to the face breadth (i 46) with advance in development, but even at the completion of growth the eyes of the gorilla have not approximated one another as much as have the eyes of the orang-utan (See Pl. VIII, fig. 2).

The excessive wrinkling around the eyes, which forms such a characteristic part of the physiognomy of the ape, is already well developed in older fetuses of the anthropoids, whereas in man accessory folds on the eyelids do not as a rule become well marked until old age. In such low races as Hottentots and Bushmen this wrinkling appears earlier, and is more accentuated than in higher races of man.

The relative width of the mouth (i 47) increases with advancing growth in the gorilla, but it is at all times greater than in man (See Pl. III, fig. 2). In regard to the lips of adult gorilla Du Chaillu (1861) states: ". . . the lips are sharply cut, exhibiting no red on the edges, as in the human face." It is very interesting to find that this difference between gorilla and man is not yet present in fetal life, since the gorilla fetuses II, III, and IV have lips at least as broad as negro fetuses and even in gorilla infants is the mucous membrane of the lower lip still

visible on the closed mouth (Pl. VII, Pl. VIII, fig. 1; and Pl. IV, fig. 1). However, there exists a difference between gorilla and human races in regard to the conditions of growth of the lips. In gorilla the lips change during development from very broad to extremely narrow, but in man they do not change, since they are either broad in fetuses and in adults, as in negroes, or narrow in early and late stages of growth, as in whites. In view of the fact that Klaatsch (1912) has expressed the opinion that the total absence of a philtrum in apes represents phylogenetically a secondary condition, it is important to state that none of the fetuses of apes showed any trace of a philtrum, nor incidentally of a tuberculum labii superioris, features which are strongly developed in man. This, of course, does not necessarily contradict Klaatsch's theory, though one might have expected indications of these structures at some prenatal stage of the apes.

There remains to be discussed in this chapter the growth of the ear. The height-breadth proportion (i 48) of the gorilla's ear varies between 58 and 71 without showing any definite growth change. The two indices (i 49 & i 49a) expressing the relative size of the ear increase greatly with advancing development. It may be said, therefore, that the ear of gorilla becomes steadily larger in proportion to the size of the head. In this respect the gorilla agrees with the chimpanzee but differs from man and the orang, in which the relative size of the ear increases at first, but decreases again in postnatal life, as has been shown by the writer in

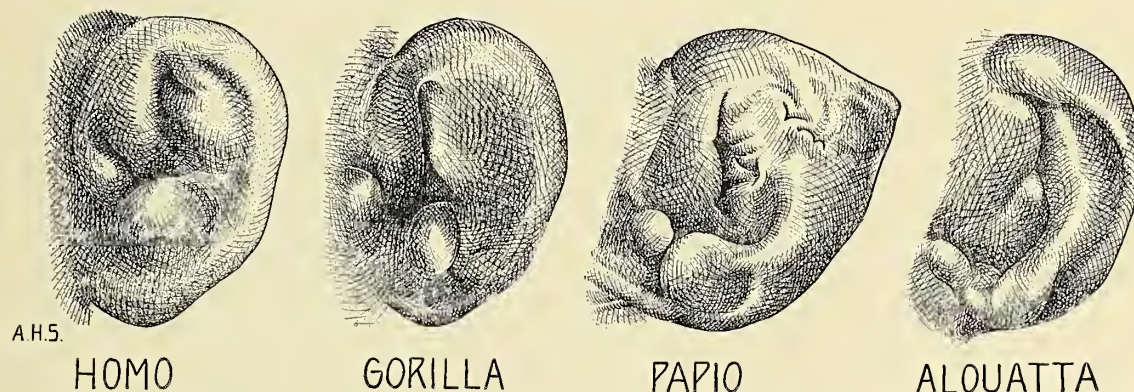


Fig. 2. Outer ears of human fetus, gorilla fetus II, baboon fetus (*Papio papio*), and howler-monkey fetus (*Alouatta palliata*); all corresponding in development to about the fifteenth week in man.

previous papers (1925 & 1926 a). The ear of the gorilla is larger than the ear of the orang, but in general smaller than the ear of the chimpanzee. Individually, however, there occur such marked variations in the size of the ear of the latter two apes, that the difference may occasionally disappear, as has been shown by Matschie (1919) and others.

The helix of gorilla fetus II is not yet rolled in. In fetus III the upper third of the edge of the helix is folded over, in fetus IV two thirds, and in the infant shown on Pl. VII the entire margin of the ear is bent in. No trace of a Darwinian tubercle can be recognized on any of the fetal or infantile ears of gorillas, though Hartmann (1880) states that it occurs occasionally in the gorilla. A glance at text figure 2 is convincing proof that the fetal ears of gorilla and man differ far less from one another than from the fetal ears of catarrhine or platyrrhine monkeys. A marked difference between the former two consists in the wide separation between tragus and antitragus in the gorilla and the close approximation of these structures in man. This distinction, however, is not constant, since in gorilla fetus III and IV tragus and antitragus almost touch one another, and in some few human ears the author found them to be as widely separated as in fetus II. Finally, attention is called to the fact that all the fetuses of gorillas possess a well developed lobule. In older gorillas such a free lobule of the ear is also frequently present (*e.g.* in the adult XVII of Ehlers, 1881) but in many cases it may be missing (Hartmann, 1880), as also may happen in man.

### PART III.

#### Chapter 11. THE BODY PROPORTIONS OF HIGHER PRIMATES IN FETAL AND ADULT LIFE.

Every part of the body is represented by the proportions listed in Table 8. A comparison between the various primates, based upon these relative measurements, can reasonably be expected to impartially take into consideration all their different specializations as well as similarities. For such a comparison it is very essential to bear in mind that all body proportions vary individually to a very considerable extent. This fact is shown, for instance, by the wide ranges of variations in the proportions of the small series of human fetuses and adults, as given in Table 8. Of the apes each type and age is represented in the table by only one specimen, the proportions of which may not be typical for the particular species and stage of development. For these reasons only marked differences between the proportions of different individual apes can be regarded as significant. Generally speaking, a difference can be relied upon as being "marked" and really significant, if it surpasses in amount the range of variation of the given proportion in a series of individuals of one of two kinds of primates compared.



TABLE 8.

The body proportions of higher primates in fetal life (at stages of development corresponding to that of gorilla fetus II) and in adult life. In the series of man the minimum, maximum, and average values are given. The indices for adult gorilla marked with \* are those of specimen XVI.

Index No.	Percentage relation between:	FETUSES							ADULTS						
		Man (series 1)			Gorilla	Chmp.	Orang.	Gib'n	Man (series 5)			Gorilla	Chmp.	Orang.	Gib'n
		Min.	Max.	Aver.	II	2.	3.	4.	Min.	Max.	Aver.	XVII	6.	7.	8.
1.	Chest circumf. (m.14) & trunk h. (m.4)	184.5	229.5	206.1	231.5	....	....	198.2	146.6	194.3	168.3	180.0*	....	157.3	167.8
2.	Shoulder br. (m.9) & trunk h. (m.4)	57.9	77.8	66.7	72.9	80.7	....	58.4	59.4	81.0	67.6	60.8	72.0	44.7	68.0
3.	Hip br. (m.10) & trunk h. (m.4)	43.9	54.3	48.9	46.3	42.4	....	39.0	54.6	68.6	61.5	....	57.0	47.7	48.8
4.	Hip br. (m.10) & shoulder br. (m.9)	64.3	86.4	73.7	63.5	52.6	....	66.9	81.3	102.3	91.2	....	79.1	106.8	71.7
5.	Trans.chest diam. (m.12) & sag. chest diam. (m.13)	113.0	133.3	120.5	109.0	....	....	111.7	120.0	154.0	130.5	....	....	114.7	117.7
6.	Shoulder h. (m.6) & trunk h. (m.4)	2.6	16.2	7.3	19.2	....	....	6.3	-0.8	+2.3	+0.1	....	....	18.8	11.2
7.	Nipple br. (m.11) & trans. chest diam. (m.12)	50.0	68.0	58.1	57.9	....	....	47.0	61.3	80.6	71.5	....	....	69.3	25.8
8.	Nipple h. (m.7) & trunk h. (m.4)	73.0	85.3	77.6	83.7	....	....	81.6	66.9	78.3	73.9	....	....	89.9	87.3
9.	Umbilicus h. (m.8) & trunk h. (m.4)	11.4	22.9	17.2	20.9	....	....	15.3	23.5	36.7	29.8	17.8	....	21.6	30.4
10.	Total upper limb l. (m.22) & trunk h. (m.4)	113.6	145.6	132.7	163.2	157.4	....	181.5	128.1	166.0	144.8	156.0	170.0	207.2	280.0
11.	Upper arm + forearm l. (m.23 + 24) & sitting h. (m.1)	40.3	47.7	43.8	52.3	50.4	74.0	71.4	61.3	70.0	64.5	....	....	81.6	105.4
12.	Upper arm l. (m.23) & total upp. limb l. (m.22)	41.6	45.5	43.6	37.7	33.5	35.8	38.5	38.5	44.9	40.7	40.6	36.5	35.6	34.6
13.	Forearm l. (m.24) & total upper limb l. (m.22)	31.2	34.0	32.7	32.1	32.9	37.4	34.9	30.8	36.1	33.9	33.6	34.0	36.0	36.9
14.	Hand l. (m.25) & total upper limb l. (m.22)	20.7	25.5	23.7	30.2	33.6	26.8	26.6	24.3	26.3	25.4	25.8	29.5	28.4	28.5
15.	Forearm l. (m.24) & upper arm l. (m.23)	69.1	80.9	75.2	85.2	98.2	104.6	90.5	76.2	92.4	83.6	82.9	93.4	101.0	106.6
16.	Hand l. (m.25) & forearm l. (m.24)	61.1	81.2	72.3	93.9	101.7	71.7	76.3	68.4	78.9	74.9	76.5	86.4	78.9	77.5
17.	Thumb l. (m.26) & hand l. (m.25)	64.0	77.3	73.0	48.0	....	....	56.5	65.1	74.3	69.2	42.7*	....	46.1	49.0
18.	Hand br. (m.27) & hand l. (m.25)	48.0	61.8	54.3	39.0	....	....	34.5	42.1	52.2	45.4	36.6*	....	30.6	23.5
19.	Total lower limb l. (m.15) & trunk h. (m.4)	105.1	132.8	116.7	107.9	106.5	....	104.6	160.8	198.5	175.4	110.8	113.7	130.1	169.5
20.	Thigh + leg l. (m.16 + 18) & sitting h. (m.1)	41.8	49.4	46.4	45.6	46.8	59.9	54.1	90.9	107.5	97.2	....	....	66.0	84.8
21.	Leg l. (m.18) & thigh l. (m.16)	65.2	84.1	75.7	78.8	90.7	103.8	77.2	74.4	91.1	84.1	88.4	90.7	89.2	91.4
22.	Foot l. (m.19) & leg l. (m.18)	71.1	95.0	81.5	106.7	98.0	98.1	92.5	65.0	73.0	68.7	97.6	102.0	118.8	91.7
23.	Foot l. (m.19) & sitting h. (m.1)	14.7	18.0	16.2	21.5	21.8	29.9	21.8	29.0	32.8	30.5	....	....	36.9	37.1
24.	Foot br. (m.21) & foot l. (m.19)	27.6	34.2	30.6	31.6	....	....	26.2	24.3	31.6	28.0	....	....	23.8	21.6
25.	Great toe l. (m.20) & foot l. (m.19)	92.7	100.0	95.9	89.0	....	....	88.6	97.3	102.4	99.8	....	....	55.9	84.1
26.	Total upper limb l. (m.22) & total lower limb l. (m.15)	108.0	120.4	113.8	151.2	147.7	....	173.4	78.7	87.6	82.5	140.7	149.2	159.2	165.0
27.	Upper arm + forearm (m.23 + 24) & thigh + leg (m.16 + 18)	87.5	102.7	94.6	114.5	107.7	123.5	131.9	63.1	71.5	66.4	115.8	116.4	123.7	124.3
28.	Upper arm l. (m.23) & thigh l. (m.16)	86.4	104.5	94.9	110.6	103.6	123.0	122.7	60.4	74.2	66.6	119.2	114.8	116.4	115.3
29.	Forearm l. (m.24) & leg l. (m.18)	88.9	107.1	94.4	119.6	112.2	124.0	143.8	57.9	71.9	66.1	111.9	118.2	131.8	134.4
30.	Hand l. (m.25) & foot l. (m.19)	73.3	96.3	83.9	105.2	116.6	90.6	118.8	68.4	77.2	72.0	80.4	100.0	87.6	113.7
31.	Aver. head circumf. (m.29) & sitting h. (m.1)	107.3	122.3	114.2	109.3	....	....	100.4	56.9	65.6	61.6	....	....	60.7	86.1
32.	Aver. head diam. (m.28 a) & sitting h. (m.1)	32.9	38.5	35.5	36.8	32.3	38.4	35.1	18.2	21.0	19.7	....	....	21.0	28.9
33.	Aver. head diam. (m.28) & trunk h. (m.4)	67.4	89.5	77.6	72.4	59.8	....	61.3	27.9	34.0	31.1	....	....	28.5	48.0
34.	Nasion—inion l. (m.31) & sagittal arc (m.35)	36.5	47.2	42.0	54.7	....	....	56.4	45.3	51.6	48.5	....	....	63.5	61.6
35.	Head br. (m.32) & head l. (m.30)	76.5	94.3	87.6	90.9	89.3	94.3	89.0	71.4	86.9	79.3	....	....	74.3	88.2
36.	Head h. (m.33) & head l. (m.30)	74.3	85.3	78.4	68.0	64.0	....	76.0	69.0	79.4	73.8	....	....	45.1	68.8
37.	Total face h. (m.39) & trunk h. (m.4)	30.8	41.4	35.7	40.4	35.9	....	28.3	20.5	26.1	23.2	....	....	25.0	31.2
38.	Upper face h. (m.40) & aver. head circumf. (m.29)	7.8	10.2	9.0	13.1	....	....	11.0	12.5	16.0	14.2	....	....	24.1	13.5
39.	Total face h. (m.39) & head h. (m.33)	45.6	62.5	52.3	70.7	79.1	....	53.8	77.2	94.3	85.4	....	....	142.2	90.7
40.	Face br. (m.41) & head br. (m.32)	80.0	89.7	84.3	86.2	....	....	84.3	75.2	95.8	90.4	....	....	100.7	86.5
41.	Upper face h. (m.40) & face br. (m.41)	30.8	41.7	37.0	47.6	....	....	39.7	46.8	63.7	55.8	....	....	74.0	50.5
42.	Nose h. (m.42) & upper face h. (m.40)	60.0	77.8	67.9	70.8	....	....	82.3	63.4	75.0	71.3	....	....	58.1	80.0
43.	Nose br. (m.43) & face br. (m.41)	20.8	28.3	25.4	45.0	....	....	20.5	22.7	26.8	24.6	....	....	27.5	19.3
44.	Nose br. (m.43) & Nose h. (m.42)	85.7	116.7	102.0	133.3	....	....	62.7	52.5	70.8	62.1	....	....	63.9	47.8
45.	Interocular br. (m.44) & Biocular br. (m.45)	40.4	50.0	45.5	40.8	....	....	40.7	29.4	38.7	33.1	....	....	26.9	29.0
46.	Interocular br. (m.44) & face br. (m.41)	29.6	37.5	34.3	28.4	....	....	33.9	19.1	27.5	23.0	....	....	14.8	20.7
47.	Mouth br. (m.46) & face br. (m.41)	30.7	39.1	34.7	45.0	....	....	52.5	31.2	41.9	35.8	....	....	54.9	53.2
48.	Ear br. (m.48) & ear h. (m.47)	50.0	71.4	59.7	67.8	....	....	81.4	44.6	58.6	51.0	62.7	....	66.7	77.8
49.	Ear h. × br. (m.47 × 48) & head l. × tot. h. (m.30 × 38)	1.8	3.0	2.5	4.7	....	....	3.8	3.9	5.8	4.7	....	....	2.5	10.0

NOTE—l.=length; br.=breadth; h.=height; trans.=transverse.

Based upon such considerations Mollison (1908) has introduced a very useful mathematical method by which it is possible to express the degree of similarity between different races or species in relation to the variability of the characters under investigation. This method is best explained by the following concrete examples. The relative length of the upper limb (i 10, Table 8) amounts to 156.0 in the adult gorilla and, on an average to 144.8 in adult man, *i.e.*, there exists a difference of 11.2 index units between the two values, which represents the absolute deviation of the one from the other. Individually this same proportion ranges in man to a maximum of 166.0, or to 21.2 index units above the average value in man. Since the value of gorilla lies above the average value in man, only the range of variation in the latter above the average ("positive range") is of interest in this case. The absolute deviation of 11.2 is now expressed in percentage of this positive range of variation in man (21.2) so that a *relative* deviation is obtained, which in this instance amounts to + 52.8. The latter figure shows clearly and precisely that the particular gorilla stands in regard to its relative upper limb-length half way between the average and maximum of this proportion in man, and that therefore these two primates do not differ significantly in regard to this character. On the other hand, the adult gibbon has a relative upper limb length of 280.0, or a value deviating from the average in man for 135.2 index units. This absolute difference amounts to 637.7 per cent of the positive range in man. Judging by the latter deviation index the gibbon differs very markedly from man in relative limb-length, indeed more than six times as much as the average differs from the maximum value in man (= 100) and more than three times as much as the minimum human variation differs from the maximum (= 200).

The deviation index can be expressed by the following formulæ:  $+ di = \frac{x - A}{ma - A} \times 100$ , in case the particular proportion to be compared lies above the average proportion of the series which serves as a basis for the comparison; or  $- di = \frac{A - x}{A - mi} \times 100$ , in case the value to be compared is smaller than the average of the series. In these formulæ *di* stands for deviation index (+ or — merely indicating the direction of the deviation from the average), *x* for the value of a given proportion in the specimen to be compared, *A* for the average of the same proportion in the series used as basis for the comparison, and *ma* and *mi* for the maximum and the minimum values of the same proportion in the same series.

The deviation indices for a number of characters can be used for the construction of deviation curves, as has been done in text-figures 3 and 4. For this purpose all the averages of the series are placed at equal distances on a straight line. At arbitrary, but equal, distances on either side are drawn two lines parallel

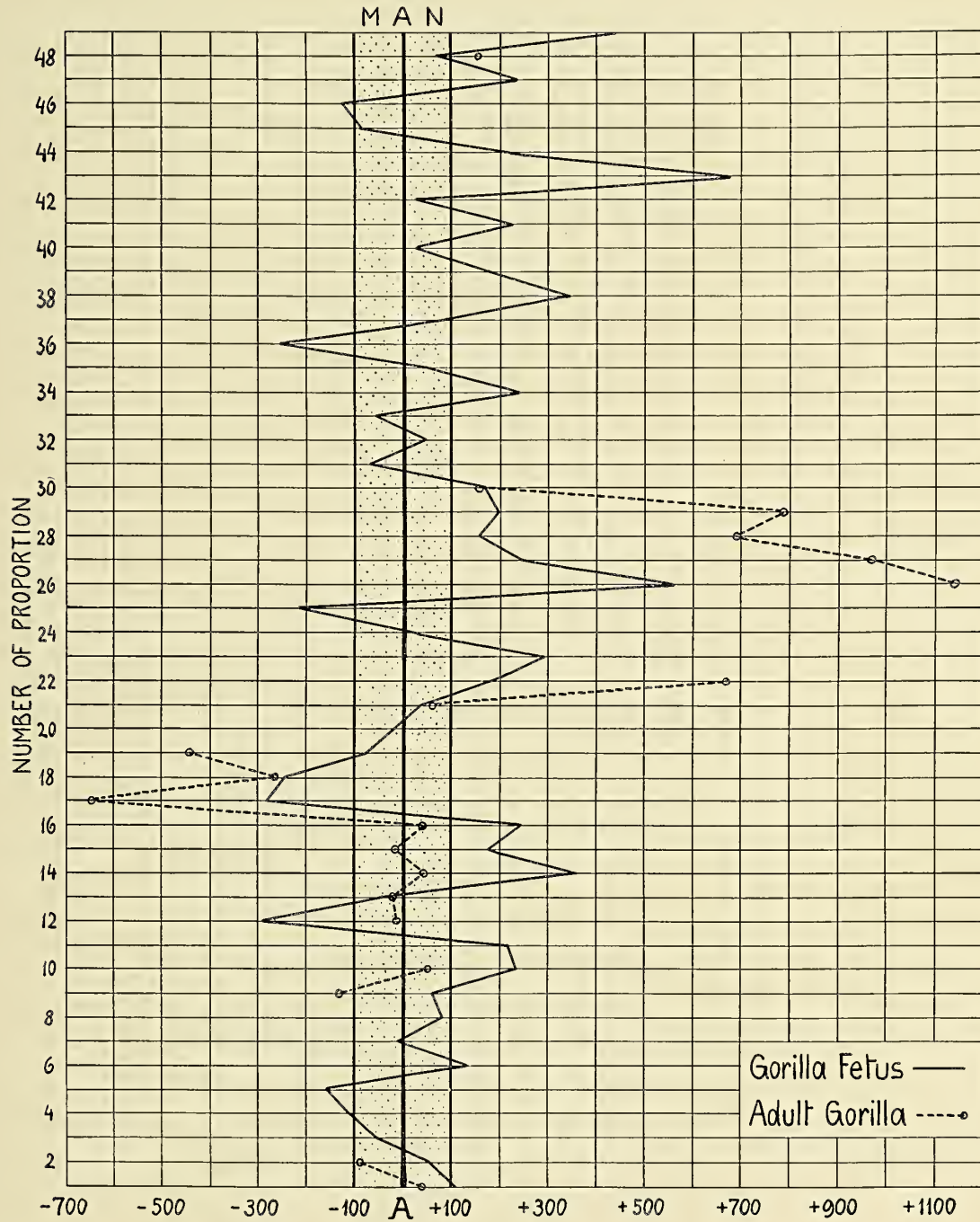


Fig. 3. Deviation curves (constructed from deviation indices in Table 9) of the proportions of gorilla fetus II and of adult gorilla XVII. The forty-nine proportions are arranged in the same sequence as they are listed in Table 8, *i.e.*, the proportion numbers, given on the left margin of this figure, correspond to the index numbers in Tables 8 and 9. The dotted area between -100 and +100 and the heavy line A represent the range of variation and the average of the proportions of human fetuses (Series 1) as well as those of human adults (Series 5), since the bases of the two curves have been superimposed on one another.

to the line of averages. These two new lines represent, and inclose between them, the ranges of variation of all the proportions of the series; their distance from the middle line is given the value of 100, which thus furnishes the scale for the plotting of the deviation curves. A curve, which would move entirely within the ribbon enclosed by the  $-100$  and  $+100$  lines, would constitute a reliable proof for the assumption that the specimen from which the curve was derived does not differ from the series used as a basis for comparison. On the other hand, should all the points of construction of a curve fall outside the lines marked 100, the specimen in question would differ in every character examined from the individuals of the series. Naturally, this difference would be the greater, the further the curve is removed from the base line *A*. It will now be understood that this method is capable of establishing and illustrating the exact relative degree of similarity between different animals in regard to their measurable characters. Furthermore, with these indices and their combination in the form of curves, it is possible to analyze the general degrees of similarity by finding readily which particular characters differ most and which others least. For instance, twenty proportions, for which data are available in both a gorilla fetus and an adult gorilla, have an average deviation index of 190.7 in the former but in the latter one of 320.5. The fetus, therefore, is in general less different from human fetuses than the adult is different from human adults. Of the various proportions, however, some show a much greater difference in degree of similarity than do others, as demonstrated by text-figure 3 (See also Table 9). Thus it is found that the proportion between the lengths of thigh and leg (i 21) has a deviation index of 36.9 in the gorilla fetus and one of 61.4 in the adult gorilla. This character, therefore, does not differ appreciably from its condition in man in fetal as well as in adult life. In contrast to this the proportion between the lengths of forearm and leg (i 29) has a deviation index in the fetus of 198.4 and in the adult of 790.0, or one nearly four times as large as the fetal value. Text-figure 3 shows also that in nineteen out of the forty-nine characters considered the fetus of the gorilla falls within the range of variation in human fetuses, and in only nineteen other characters does it differ from the human average more than the human minimum variation differs from the maximum variation, *i.e.*, it has deviation indices above 200.

In text-figure 4 the deviation curves of the various primate fetuses are compared with each other. A study of these curves leads to three general conclusions of considerable importance. First of all, it can be seen at a glance that by and large all the curves maintain a surprisingly similar course. In other words, in the great majority of characters all the fetuses of apes deviate from the human fetal

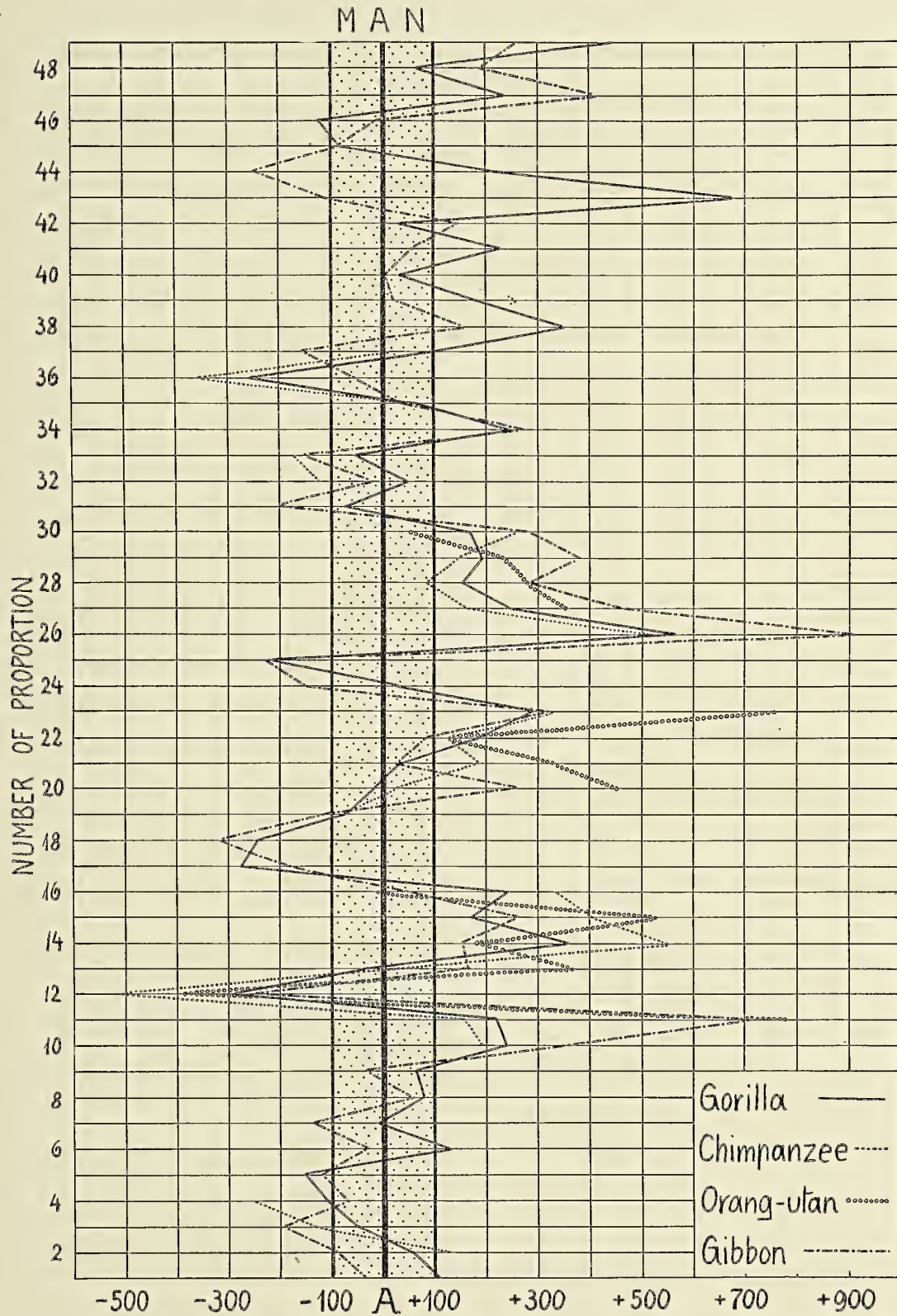


Fig. 4. Deviation curves of the proportions of the ape fetuses in Table 8. The dotted area represents the range of variation, and the heavy line A the average of the proportions in Series 1 of human fetuses.

condition in corresponding directions, *i.e.*, either all to the right or all to the left. This must be interpreted as indicating, that in regard to most proportions, man represents one extreme among the higher primates, the opposite extreme being formed by one or another of the apes. In other words, the human proportions fall rarely within the range of different values of the same characters among the apes. These statements, however, do not imply that man is in most respects further removed from the apes than are some apes from others. Many examples could be mentioned to show that there exist much greater gaps between one ape and another ape than between man and some ape. To quote just two instances in support of this last assertion: The proportion between the lengths of forearm and upper arm (i 15) has a deviation index in the fetus of the gorilla of only + 175.3, but in the fetus of the orang-utan one of + 516.0; the deviation index for the relative foot-length (i 23) amounts in the fetus of the gorilla to + 294.2 but in the fetus of the orang-utan to + 761.5. In regard to both these proportions man and gorilla differ very much less than do the gorilla and the orang.

The second conclusion based upon text-figure 4 consists in the interesting fact that by far the most marked deviations of the curves are found in the proportions of the limbs (i 10 to i 30) and the smallest deviations in those of the trunk (i 1 to i 9), whereas the proportions of the head (i 31 to i 49) occupy in general an intermediate position in this respect. It can be stated, therefore, that the various diverging evolutionary specializations of the higher primates must have affected the limbs much more than the trunk.

Finally, as a third conclusion it may be mentioned that in general the fetus of the gorilla deviates to a lesser degree from human conditions than do the fetuses of the other apes. Of this more will be said later on.

TABLE 9.  
Deviation indices of the body proportions of the fetal and adult primates listed in Table 8.

Index No.	FETUSES				ADULTS			
	Gorilla II.	Chimpanzee 2	Orang 3	Gibbon 4	Gorilla XVII	Chimpanzee 6	Orang 7	Gibbon 8
1.	+108.5	.....	.....	-36.5	+45.0	.....	-50.7	-2.3
2.	+55.8	+126.1	.....	-94.3	-82.9	+32.8	-279.3	+3.0
3.	-52.0	-130.0	.....	-197.8	.....	-65.2	-200.0	-198.5
4.	-108.5	-224.6	.....	-72.4	.....	-122.3	+140.5	-197.0
5.	-153.3	.....	.....	-117.2	.....	.....	-150.3	-121.9
6.	+133.7	.....	.....	-21.2	.....	.....	+850.3	+505.0
7.	-2.5	.....	.....	-137.0	.....	.....	-21.6	-448.0
8.	+79.2	.....	.....	+51.9	.....	.....	+363.5	+304.5
9.	+64.9	.....	.....	-32.8	-126.9	.....	-130.0	+8.7
10.	+236.2	+191.4	.....	+378.1	+52.8	+118.8	+294.3	+637.7
11.	+217.8	+169.1	+774.5	+708.0	.....	.....	+311.0	+744.0
12.	-295.0	-505.0	-390.0	-255.0	-4.5	-190.8	-232.0	-277.2

Index No.	FETUSES				ADULTS			
	Gorilla II.	Chimpanzee 2	Orang 3	Gibbon 4	Gorilla XVII	Chimpanzee 6	Orang 7	Gibbon 8
13.	- 39.9	+ 15.4	+361.5	+169.1	- 9.7	+ 4.5	+ 95.5	+136.3
14.	+361.0	+550.0	+172.1	+161.0	+ 44.4	+455.5	+333.3	+344.5
15.	+175.3	+403.3	+516.0	+268.0	- 9.5	+111.2	+197.8	+261.3
16.	+242.7	+330.2	- 5.4	+ 44.9	+ 40.0	+287.5	+100.0	+ 65.0
17.	-277.8	.....	.....	-183.3	-646.0	.....	-563.5	-492.5
18.	-242.8	.....	.....	-314.2	-266.3	.....	-448.7	-664.0
19.	- 75.8	- 88.0	.....	-104.2	-442.3	-422.3	-310.0	- 40.4
20.	- 17.4	+ 13.3	+450.0	+256.4	.....	.....	-495.0	-196.9
21.	+ 36.9	+178.5	+334.5	+ 17.9	+ 61.4	+ 94.3	+ 72.9	+104.2
22.	+186.6	+122.2	+123.0	+ 81.6	+672.0	+774.7	+1164.0	+535.0
23.	+294.2	+311.0	+761.5	+311.0	.....	.....	+234.7	+286.9
24.	+ 27.8	.....	.....	-146.5	.....	.....	-113.5	-172.8
25.	-215.5	.....	.....	-228.0	.....	.....	-1755.0	-628.0
26.	+566.6	+514.0	.....	+903.0	+1140.0	+1307.0	+1504.0	+1616.0
27.	+245.5	+161.8	+356.8	+460.5	+969.0	+980.0	+1123.0	+1134.0
28.	+163.6	+ 90.6	+292.9	+289.7	+692.0	+634.0	+655.0	+640.6
29.	+198.4	+140.2	+233.0	+389.0	+790.0	+898.0	+1132.0	+1176.0
30.	+171.7	+263.8	+ 54.0	+281.4	+161.3	+538.5	+300.0	+802.0
31.	- 71.0	.....	.....	-200.0	.....	.....	- 19.2	+612.8
32.	+ 43.3	-123.0	+ 96.7	- 15.4	.....	.....	+100.0	+707.0
33.	- 51.0	-174.5	.....	-159.8	.....	- 81.2	+127.5	+583.0
34.	+244.2	.....	.....	+277.0	.....	.....	+484.0	+423.0
35.	+ 49.2	+ 25.4	+100.0	+ 29.0	.....	- 63.3	+117.0	+ 76.3
36.	-253.6	-351.2	.....	- 58.5	.....	-597.7	-104.1	-327.0
37.	+ 82.4	+ 3.5	.....	-150.8	.....	+ 62.1	+400.0	+275.7
38.	+341.2	.....	.....	+166.7	.....	.....	+550.0	- 41.2
39.	+180.3	+262.8	.....	+ 14.7	.....	+638.2	+439.5	+ 59.5
40.	+ 35.2	.....	.....	0	.....	.....	+190.8	- 25.6
41.	+225.6	.....	.....	+ 57.5	.....	.....	+230.5	- 58.9
42.	+ 29.3	.....	.....	+145.4	.....	.....	-167.0	+235.0
43.	+676.0	.....	.....	-106.4	.....	.....	+131.8	-278.9
44.	+212.8	.....	.....	-241.0	.....	.....	+ 20.7	-149.0
45.	- 92.1	.....	.....	- 94.1	.....	.....	-167.5	-110.7
46.	-125.4	.....	.....	- 8.5	.....	.....	-210.5	- 59.1
47.	+234.1	.....	.....	+404.5	.....	.....	+313.0	+287.0
48.	+ 69.2	.....	.....	+185.5	+154.0	.....	+206.5	+352.7
49.	+440.0	.....	.....	+260.0	.....	.....	-275.0	+482.0
AVER.	173.5	210.3	313.9	189.5	320.5	385.5	364.8	365.1

The deviation indices of all the proportions contained in Table 8 are listed in Table 9. By figuring averages from these indices it is possible to compare the relative degrees of similarity of the different primates in a condensed and clear manner. Such averages, however, can as yet be only preliminary and tentative, inasmuch as data for many proportions in several of the apes are still wanting. For the same reason it was necessary to calculate more than one average from each column in Table 9. It must also be mentioned that the absolute size of these averages is naturally meaningless in itself, since it is dependent entirely on the

number of characters upon which it is based.<sup>25</sup> However, such average deviation indices, as are derived from the same proportions in different apes, are of considerable value for comparisons, since they furnish an impersonal scale for the evaluation of the *relative* amount of difference between the various higher primates. In general these averages become the more reliable and representative, the greater the number of characters considered.

An attempt is made first of all to answer by means of these averages the question whether the apes are less removed from man in fetal than in adult life. The following data are available for this purpose.

Average deviation indices based upon the greatest number of proportions which are known in both the fetus and the adult of a given ape:

Gorilla (twenty proportions): fetus 190.7; adult 320.5.

Chimpanzee (twenty-two proportions): fetus 220.6; adult 385.5.

Orang-utan (sixteen proportions): fetus 313.9; adult 416.5.

Gibbon (forty-nine proportions): fetus 189.5; adult 365.1.

In the gibbon, the only ape in which all forty-nine proportions are available for fetus and adult, the maximum deviation index equals 903 in the fetus and in the adult 1616. In the former 35 per cent of all the proportions have deviation indices above 200 whereas in the latter this percentage has increased to 59.

All these figures demonstrate very clearly and without any exception, that in regard to their body proportions the fetal apes are much more similar to human fetuses than are the adult apes to adult men. This is also evident from the data collected in Table 10, which, however, are based upon a smaller number of proportions (all appertaining to the limbs). The figures in this table refer in every case to the same proportions, so that they permit not only a comparison between the values for fetal and adult life in one and the same ape, but also one between the values of the different apes. The average deviation indices in Table 10, just as the above listed averages, are much larger in the adults than in the fetuses (See also text-figure 5). The maximum deviation indices, likewise, attain much higher values in the former than in the latter. These figures, furthermore, show that the differences between the degrees of deviation of the various apes from man are not yet as marked in fetal as in adult life. The average deviation indices range in the fetuses only between 192 and 258, but in the adults from 314 to 498. This greater

<sup>25</sup> These averages are furthermore influenced by the extent of the range of variation in the series, which serves as a basis for comparison. For instance, the average range of variation of all the proportions amounts in the series of human fetuses to 14.6, but in the series of human adults to only 12.9. Theoretically it could be expected, therefore, that, if the series of adults had a range of variation equal to that of the series of fetuses, the deviation indices of the adult apes would be reduced for 11.6 per cent of their actual amounts.



uniformity in the relative deviations of the fetuses than in that of the adults is graphically shown by the concentric semi-circles of the diagram in text-figure 5.

No alternative seems possible in the interpretation of these findings. The

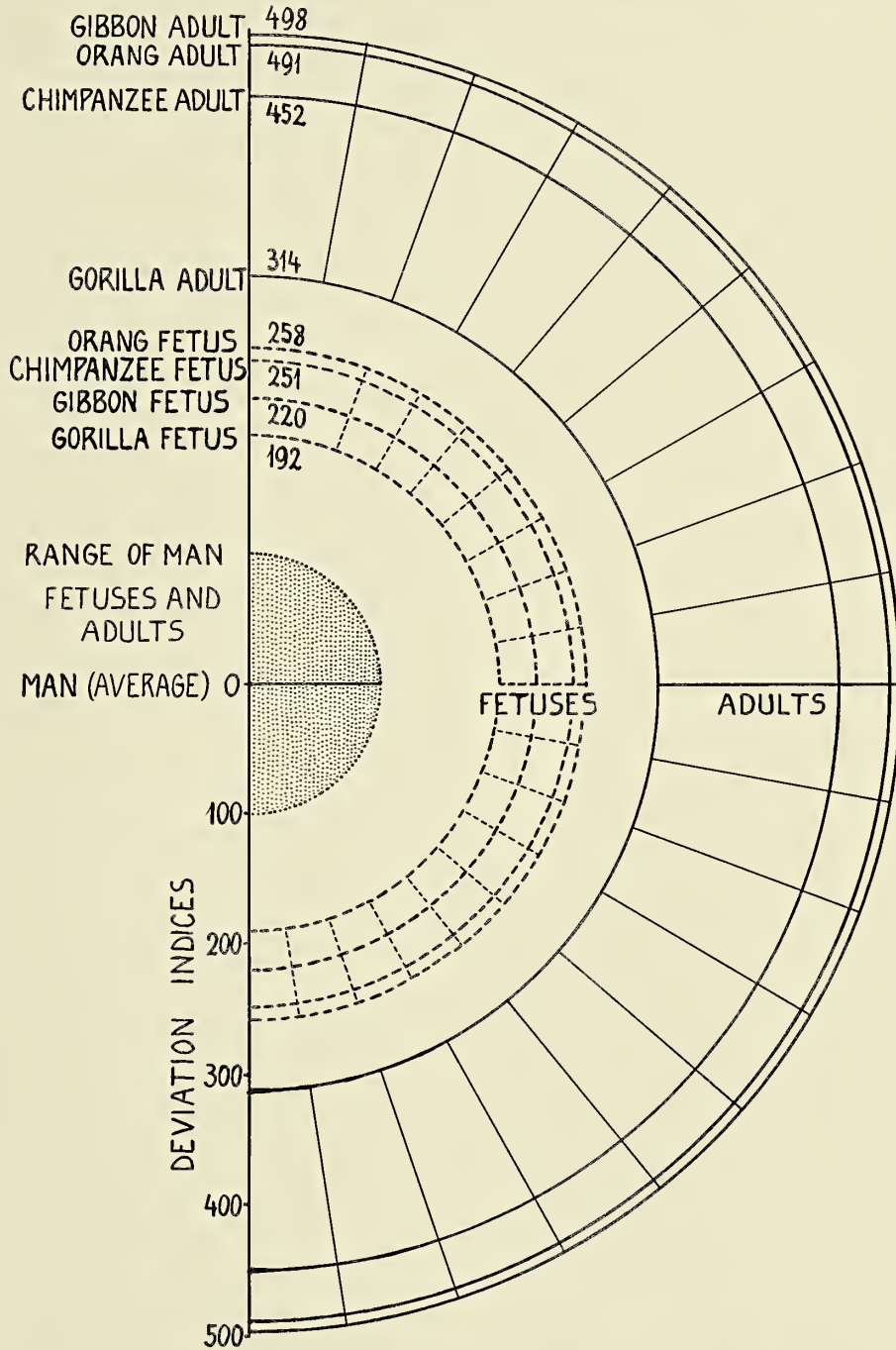


Fig. 5. Diagrammatic representation of the average deviation indices, listed in Table 10. These averages form the radii of the concentric semi-circles. Note that all the adult apes are further removed from man than are any of the fetal apes and that the circles for the fetuses are closer together than those for the adults.

higher primates are more closely alike in early than in later stages of growth, since they all inherited the same developmental process from one common ancestral stock, a process which could have become altered only after their separation into diverging branches. Just as the various specializations became more and more accentuated with advancing evolution of the species, so do the differences between the different primates become in general more and more marked with advance in individual development. Similar statements have been made many times before, but these had always been based upon impressions alone. The correctness of the latter is now proved by means of figures. Thus it can be said that the age-changes in the average and maximum deviation indices constitute a new support for an old hypothesis, namely for the recapitulation theory. These age-changes show nothing more nor less than that the increasing phylogenetic specializations are in general repeated and paralleled by increasing ontogenetic differentiations. These conditions could not be understood and explained without the assumption of one origin for all the higher primates.

TABLE 10.  
Deviation indices of the eleven body proportions which are available in  
all the fetal and adult primates listed in Table 8.

		Average Deviation index	Maximum Deviation index	Percentage of Deviation indices above 200
Gorilla	fetus	192.4	361.0	36.4
	adult	314.0	969.0	36.4
Chimpanzee	fetus	251.0	550.0	45.5
	adult	451.7	980.0	63.6
Orang-utan	fetus	258.1	516.0	63.6
	adult	491.4	1164.0	63.6
Gibbon	fetus	219.9	460.5	54.5
	adult	497.8	1176.0	72.7

Another deduction, reached from the figures in Table 10 and their diagrammatic representation in text-figure 5, carries the last conclusion a step further, inasmuch as it indicates the proportionate degrees of separation which the various primates have reached in the course of their divergent evolution from a common source. All the data agree in the fact that gorilla possesses in fetal as well as in

adult life the lowest deviation indices of all apes. The gibbon, curiously enough, ranks next in the fetal stage, but at the completion of growth it has not only the highest average and maximum deviation indices among all the apes, but also the greatest percentage of indices above 200. If a greater number of proportions than that used in Table 10 is considered, the relative degrees of similarity of the various apes do not change materially in adult life, but among the fetuses the gibbon is shifted from second to third place. These new and somewhat more representative values are given below.

Average deviation indices of adult apes, based upon the fifteen proportions which are available in all adults:

Gorilla	Chimpanzee	Gibbon	Orang-utan
304.5	456.7	518.2	519.5

Again it is the gorilla, which according to these figures stands nearest to man, whereas the orang-utan and the gibbon, with practically the same averages, show the greatest differences from human conditions. The chimpanzee, which in this respect occupies an intermediate position, is by the above average somewhat further removed from the Asiatic apes than it is by its average in Table 10.

Average deviation indices of ape fetuses based upon the sixteen proportions available in the orang-utan fetus:

Gorilla	Chimpanzee	Gibbon	Orang-utan
171.2	212.7	233.6	313.9

Average deviation indices of ape fetuses, based upon the twenty-six proportions available in the chimpanzee fetus (leaving out the orang-utan fetus):

Gorilla	Chimpanzee	Gibbon
169.3	210.3	225.8

The twenty-six body proportions, which have been used for the last figures, differ on an average between the gorilla fetus and the average human fetus for 169 per cent of the difference between the average and maximum values of these proportions in man. This means that the particular gorilla stands in regard to these twenty-six characters closer to the most extreme human variation than the latter stands to the human average.<sup>26</sup> If the difference between extreme and average equals 100, then that between gorilla and human extreme amounts to only 69. The difference between the gorilla and the gibbon fetus is on the same scale 57 (226 minus 169). Based upon these simple calculations it can be stated that there

<sup>26</sup> To find an individual which possesses in every one of the proportions the extreme variation thereof is, of course, as improbable as it is that there should exist some other individual representing a combination of the average conditions of all proportions. With these facts in mind it is readily understood that the above generalizing deductions can have only a theoretical value.

exists nearly as small a difference between a gorilla fetus and the most extreme human fetus as between the former and a gibbon fetus.

It can hardly be regarded as a mere chance occurrence that the greatest average deviation indices are found in the exclusively arboreal apes, the gibbon and orang-utan, whereas the lowest index coincides with the least arboreal type, the gorilla. It can be predicted without any risk, that, if a series of oranges or of gibbons should ever be used as a basis for deviation indices in the other higher primates, the most terrestrial form, man, would show the highest indices and the largely terrestrial gorilla the second highest.

It remains to consider in a brief and preliminary way the important problem whether the various primates differ in regard to the relative amount of ontogenetic change in their body proportions. This question can be answered by means of the following method applied to the figures in Table 8. If the difference between the values of a proportion in fetal and in adult life is calculated in percentage of the value of this proportion in the fetus, an index is obtained which expresses the relative amount of ontogenetic change in this proportion. It was shown by the author in a previous paper (1926 b) that the degrees of developmental change vary widely in different proportions, *i.e.*, whereas some proportions may remain almost unaltered throughout growth, others may change very profoundly. For generalizing statements it is essential, therefore, to figure averages from the relative amounts of ontogenetic change in the various proportions.<sup>27</sup> From all the forty-nine proportions such averages can be formed only in man and in the gibbon. In the former it is found to amount to 32.2 and in the latter to 24.8. This means that on an average the forty-nine human proportions increase or decrease during growth for 32.2 per cent of their values in the fetus, whereas the same proportions of the gibbon change for only 24.8 per cent of their initial values.

The average relative ontogenetic changes in the eleven proportions, which are available in all primate fetuses and adults, show the following values:

Man	Gorilla	Chimpanzee	Gibbon	Orang-utan
23.4	9.8	7.9	7.7	6.7

According to these last figures, which are based exclusively upon limb proportions, man changes in the course of growth much more extensively than any of the apes. It is also noteworthy that of all the apes gorilla comes nearest to man in

<sup>27</sup> The average relative ontogenetic change is expressed by the following formula:

$$\left[ \sum \frac{fx - ax \text{ (or: } ax - fx)}{fx} \times 100 \right] : n$$

*fx* = value of a proportion in the fetus; *ax* = value of the same proportion in the adult of the same primate species; *n* = number of proportions considered.

this respect. In all of the apes the limb proportions change ontogenetically on an average for less than one-tenth of their values in fetal life, but in man this change amounts to nearly one-fourth of the fetal values. To find this marked contrast between the apes on the one hand and man on the other is rather unexpected. This result encourages further investigations of this important problem. It is not at all unlikely that it will be possible to demonstrate a direct connection between the amount of ontogenetic change and the duration of growth. At present it must suffice to point out that among higher primates it is one and the same form—man—which has its proportions changed most extensively during development and which possesses the longest period of growth, by which, one may add, it has become possible to accomplish these unique changes.

Finally, it should be mentioned that the above data do not agree with the recent stimulating theory of Bolk (1926 a & b) which supposes that man is distinguished from the apes by retaining fetal conditions more closely than do the latter. In regard to most body proportions just the opposite seems to be the case, as shown by the following two examples in addition to the averages discussed above. The important relation in length between upper and lower limb (i 26, Table 8) changes in man from 114 in the fetus to 82 in the adult, or for 28.1 per cent of the fetal value, but in gorilla it changes only from 151 in the fetus to 141 in the adult, or for only 6.6 per cent of the fetal value which is less than one fourth the relative amount in man. The proportion between the size of head and trunk (i 33) decreases in man from 78 in the fetus to 31 in the adult, or for 60.3 per cent of the former value. In the gibbon the same proportion drops only from 61 to 48, *i.e.*, for only 21.3 per cent of the index in the fetus. In both these instances the apes retain the fetal condition much more closely than does man.

#### PART IV.

##### Chapter 12. SUMMARY AND CONCLUSIONS.

The results obtained from this study refer to a wide variety of topics with frequently little, if any, connection between the points discussed. This paper, therefore, can not claim to present a coherent picture of the conditions of growth in gorilla and other higher primates. It constitutes merely a first attempt to bring together the previously scattered observations of other authors and to fill, as far as possible, some of the gaps in this collected information. This effort shows first of all how little exact knowledge of the ontogeny of apes is really as yet available, and how much more material and study will be necessary before all the outlines at least of this important chapter of science can be definitely established.

The following enumeration of the most noteworthy data, derived from the present investigations, deals in part with final and amply supported facts, but in part also with only tentative findings, requiring corroboration from observations on additional specimens.

*General conditions of growth.*

The African apes grow more slowly than man before birth but much more rapidly during postnatal life. The total period of growth is very much shorter in apes than in man and the relative amount of growth-change in body-proportions is markedly less in the former than in the latter.

*Body surface.*

The first pigment of the skin of higher primates appears often in localized zones. The color of the skin develops earlier in the orang and the chimpanzee than in the gorilla. The latter occupies an intermediate position in this respect between the former and the negro. In all the apes and in negroes the final and darkest color of the skin is not attained until shortly after birth.

As in man, the first hair of the gorilla appears on the eyebrows, lips and chin; the eyelashes and the hairs on the scalp develop slightly later. Man, the gorilla, and the chimpanzee have in common the fact that during late fetal life and earliest infancy the hair on the scalp is very much longer than on the rest of the body. In new-born lower primates there exists no such difference between the length of the hair of the head and that of the hair on the body.

The ischial callosities of catarrhine monkeys develop relatively early in fetal life and before any hair has appeared over the ischial tuberosities. In the gibbons these callosities appear at a much later stage of growth, replacing a coat of very short hair. The latter disappears late in fetal life from two symmetrically placed zones. Not until shortly before birth does the skin of these zones begin to become callous. Such hair-free zones have been observed in an older chimpanzee fetus. In rare cases anthropoid apes may still possess ischial callosities. These are less developed and less frequent in the gorilla than in the chimpanzee and orang, indeed, in the gorilla they may really no longer deserve the term "callosity". Another kind of callosity, one which occurs in connection with their special mode of walking, is found in the gorilla and the chimpanzee on the middle segments of the fingers. These callous places and the associated lack of hair over the middle phalanges have been found in fetuses of both these apes and are, therefore, hereditary characters.

The coccygeal tubercle, the last ontogenetic remnant of an outer tail, disap-

pears at a much earlier stage of development in man and gibbon than in the gorilla, orang, and chimpanzee. Among the last three apes this structure persists for the longest period in the chimpanzee and for the shortest in the gorilla.

In the females of all the higher primates the labia majora are well developed in fetal life, but, whereas they persist in man and the gibbon throughout life, they undergo during postnatal growth a process of nearly, or even entirely, complete reduction in the three large apes.

Accessory folds on the eyelids of anthropoids and the marked general wrinkling of the skin in the region of the eyes develop in apes during fetal growth. In man, on the other hand, such wrinkling does not appear until very late in life, if it occur at all.

The lips of gorilla fetuses are still as broad as in negro fetuses, but in the former this condition does not persist as in the latter.

#### *Body proportions.*

Of all the body proportions those of the limbs show the greatest differences among the various higher primates, whereas those of the trunk are most similar in apes and man. The relative circumference and widths of the trunk of higher primates decrease in general with advancing development. In the gorilla there seems to exist a tendency to increase the relative girth of the chest late in growth. The trunk of lower primates is long and slender, but that of apes and man is proportionately broad and stout and even more so in the gorilla than in man.

The length of the upper limb in relation to the height of the trunk increases in most primates during the first part of growth but decreases slightly during the second part. The lower limb-length of the gorilla grows somewhat faster than the height of the trunk and also slightly faster than the length of the upper limb. *Gorilla beringei* has on an average somewhat shorter upper and somewhat longer lower limbs than has *Gorilla gorilla*. In gorilla the forearm is relatively shorter than in any other ape. It is especially short in *Gorilla graueri*, which equals man in regard to the humerus-radius proportion. The hand of the adult gorilla is relatively shorter and broader than that of other apes and equals in these respects the human hand. In regard to the relative size of the thumb the adult gorilla, particularly *Gorilla beringei*, resembles human conditions more closely than do other apes. The foot of the adult gorilla is extremely broad; the heel is broad and prominent; the great toe reaches relatively far forward; and the lateral toes are relatively short. In all these features gorilla approaches man more closely than do other apes. In *Gorilla beringei* the great toe and the sole extend proportionately further forward than in *Gorilla gorilla* and the cleft between toes I and II as well

as the lateral digits are shorter in the former than in the latter. In the gorilla fetus the hand as well as the foot is of a much more arboreal character than it is at the completion of growth. Both hand and foot are relatively longer and more slender, the thumb as well as the great toe is proportionately shorter, and digits II to V are proportionately longer in the fetus than in the adult.

The size of the head decreases with advancing growth in proportion to the size of the trunk in the gorilla as well as in all other primates. Fetuses of apes and man have extremely broad heads, *i.e.*, very high cephalic indices. The nose is as prominent in gorilla fetuses as in negro fetuses and it projects more in all later stages of growth in the gorilla than in the other apes. The ear of gorilla increases with advancing development in relation to the size of the head.

*Comparisons based upon deviation indices.*

In regard to body proportions man rarely falls within the range of the different values for the same character among the apes, but most frequently represents one extreme of the total range of all higher primates. Within the latter range, however, there exist just as marked differences between one ape and another ape as between some one ape and man. The resemblance between the various higher primates is much greater in fetal than in adult life. Fetuses do not as yet show the wide divergences of adults, but are much more uniform in regard to body proportions than the latter. Of all the apes gorilla resembles man most closely, both in fetal and in adult life. The chimpanzee ranks second in this respect, whereas the two strictly arboreal apes, the orang and gibbon, are much further removed from man than are the African apes.

The statement in the last paragraph, that there exists a greater similarity between man and gorilla than between man and any of the other apes, is supported not only by the average and maximum deviation indices, but also by many other findings of the present study. Some of these corroborative findings, which are not considered in the deviation indices, may be briefly reviewed again: Ischial callosities are no longer present in man; they may be merely indicated in the gorilla in very rare instances; but in the chimpanzee and orang they are still quite well developed in occasional specimens. The color of the skin of the gorilla develops somewhat earlier than that of the colored races of man, but in the chimpanzee the skin begins to darken at a still earlier stage than in the gorilla. The relative amount of ontogenetic change is greatest in man, but in gorilla it is greater than in the other apes. Horizontal sections through the nasal region of the skull are straight, indicating a flat nose in the gibbon, orang, and chimpanzee; but they are curved forward, according to the prominence of the nose, in the gorilla and



man. The size of the gorillan ear is in general quite similar to that of the human ear; whereas the ear of the orang is very much smaller, and the ear of the chimpanzee very much larger, than the ears of the former two primates. The points of similarity in the hand and foot of man and the gorilla, particularly of *Gorilla beringei*, are too numerous and detailed to repeat here. There can be no doubt that in regard to hand and foot no other ape can rival the gorilla in its claim to being least different from man. Last, but not least, must be mentioned that in general mode of life man, the exclusively terrestrial primate, has become far removed from the apes. Again, however, it is the gorilla which differs in this respect from man to a lesser degree than do the other forms, since the adult gorilla is largely terrestrial, the chimpanzee largely arboreal, and the orang as well as the gibbon extremely arboreal.

That the last mentioned distinctions were much less pronounced in the past, and did not as yet extend to the extreme modes of life, may be concluded from certain ontogenetic conditions, particularly from those appertaining to the limbs. Observations on human fetuses, published by the author in previous papers (1924 a, 1925, 1926 b), justify in his opinion the conclusion that man's evolutionary course must have passed from arboreal through semi-terrestrial to extremely terrestrial phases. On the other hand, the as yet unfinished studies of the author on the growth of the orang-utan and the gibbon permit the preliminary deduction that the *extreme* adaptations to tree-life, which distinguish these apes, had not yet been developed in earlier phases of their phylogeny. Finally, the present investigation has produced evidence in support of the assumption that the gorilla has changed comparatively recently from an arboreal to a largely terrestrial mode of life. It has been shown that the hand and the foot of gorilla possess in late fetal stages most of the features typical of arboreal, though not extremely arboreal, primates. Even in gorillan infants these structures are not yet nearly as much modified for terrestrial use as in adults. Furthermore, in the adult of this ape the arms are proportionately shorter and the legs relatively longer than in the young animal. This all rather strongly suggests that, while attaining its unique colossal size, which rendered tree-life impracticable, the gorilla swerved in its evolutionary trend toward that which was most likely followed by the human precursors. This change seems to have been somewhat more pronounced, or to have been more accelerated, in *Gorilla beringei* than in the West African gorillas. In this connection there should be quoted a conclusion reached by Gregory (1916), with which the above statement agrees very well, but which points out in addition the important inherent limitations to the evolutionary course of the gorilla: "In

adopting a partly terrestrial habit the gorilla has entered upon a line of adaptation which in the forerunners of man resulted in a fully bipedal, cursorial type, capable of invading the plains. But, as the gorilla is largely frugivorous and limited to the forests and their neighborhood, the only course left for it (apart from its inevitable extinction by man) would have been to go on increasing still further in size, until it might have surpassed even the Kadiak bear in bulk. Such a beast might have ambled along on all fours, partly supporting itself upon its knuckles as the gorilla now does."

The particular conclusion that the difference between man and gorilla is less than that between man and other apes does not necessarily imply that man

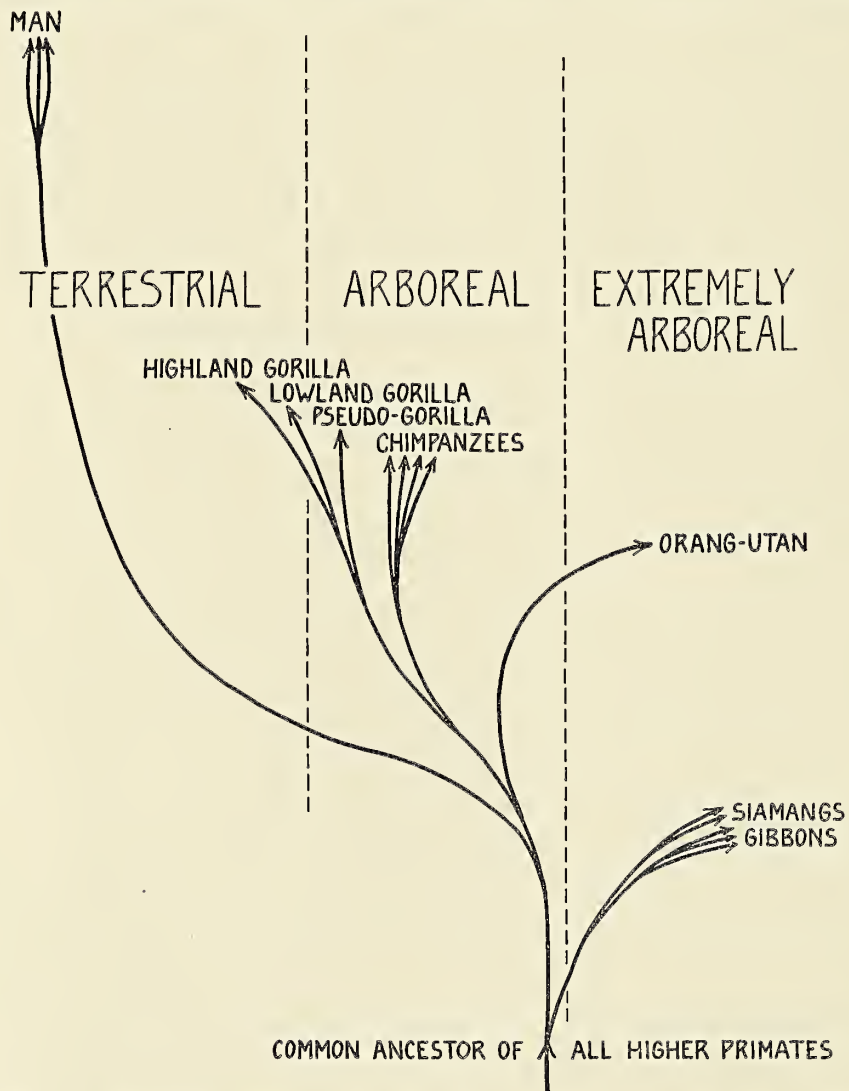


Fig. 6. Hypothetical pedigree of the recent higher primates, as supported by the results of this paper. The branching lines indicate in their directions and relative lengths the probable degrees of divergence in the various evolutionary trends and the proportionate amounts of general departure from the common ancestral form.

descended from gorilla-like forms, nor that a common ancestor of the two resembled the gorilla, though such structures as the foot and such proportions as that between the lengths of upper and lower limb were most likely gorilla-like in some stage of man's evolution. It must mean, however, that the evolutionary courses of man and the gorilla diverged to a lesser degree than did the ascending paths of man and the other apes. All the higher primates must have undergone far-reaching changes since they spread from a common source. For reasons to discuss which here would lead too far, the author is inclined to the view that in many respects (excluding all the *extremely* arboreal specializations) the gibbons departed least from the ancestor of all the higher primates and even stand closest of all recent primates to the hypothetical form which links man with the three large apes. These ideas are represented in diagrammatic form in text-figure 6. It must be stated emphatically that this particular pedigree is based principally upon body proportions and the other topics discussed in this paper. As has been mentioned in the introduction, the final family tree will have to consider the evidence from all the fields of biology. It will, therefore, represent to a certain degree a critical compromise between all the pedigrees suggested independently by different specialists. Naturally, the last word will have to be granted to paleontology, even though its testimony be restricted to the skeleton and the teeth.

The particular pedigree, proposed here, agrees in principle with that published by Keith (1925); but differs slightly from those of Gregory (1916), Sonntag (1924), and others, inasmuch as according to the latter pedigrees, the orang branches off before man does, and according to the diagram here given this relation is reversed. The author's diagram is based upon the study of recent primates alone, from which it seems at present impossible to abandon the view that in general the three large apes are linked somewhat more closely together than man and the African apes.

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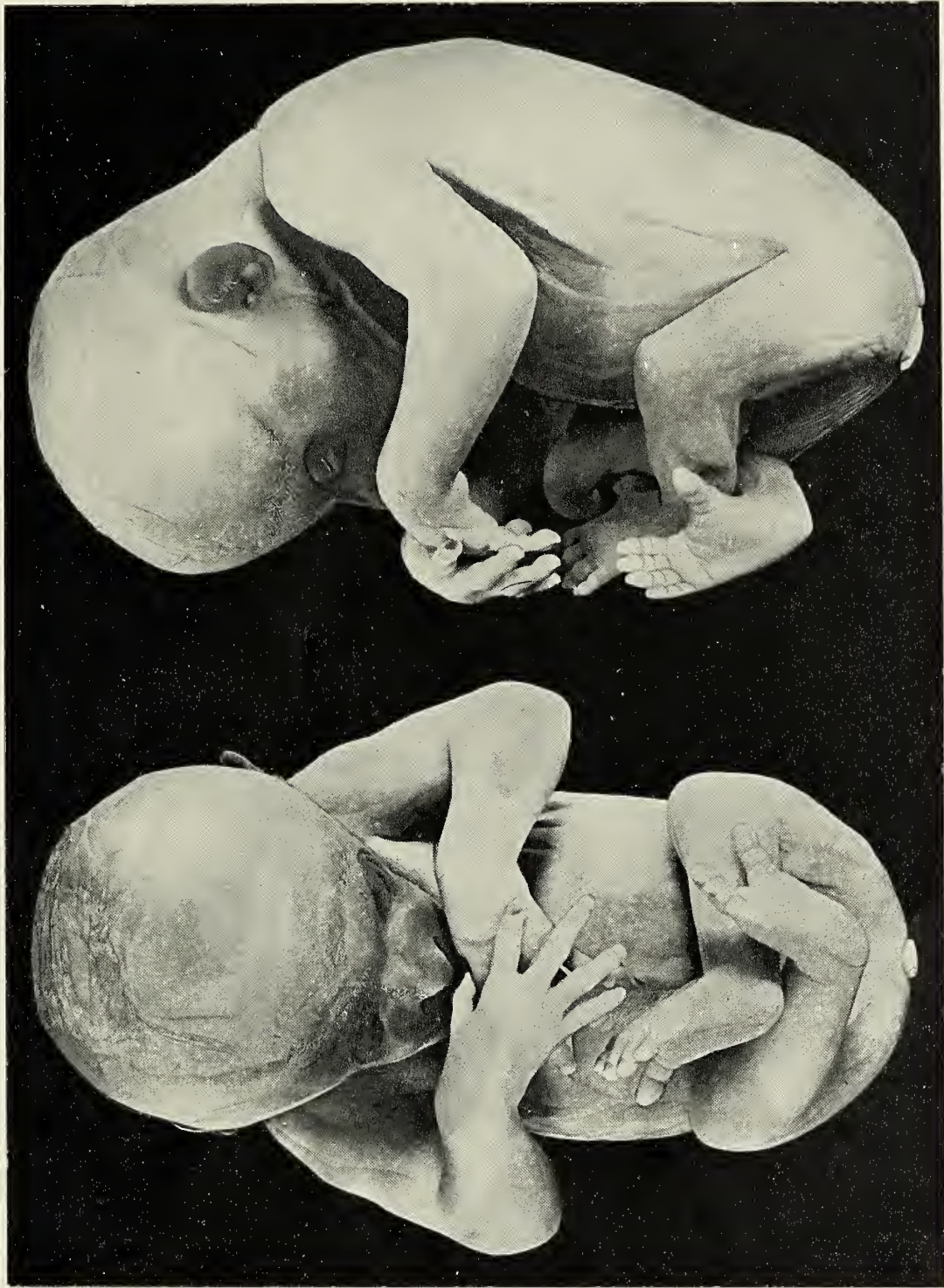
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EXPLANATION OF PLATE I

Front and side view of Gorilla Fetus II (approximately natural size.)  
Car. Mus. Acc. No. 7698.





Gorilla Fetus II. Natural Size.

## EXPLANATION OF PLATE II.

- FIG. 1. Front view of Gorilla Fetus V (after Anthony, 1918).  
FIG. 2. Side view of Gorilla Fetus III (after Deniker, 1885).  
FIG. 3. Gorilla VI at the approximate age of one month, with its negro nurse, (after Reichenow, 1921).



1



2



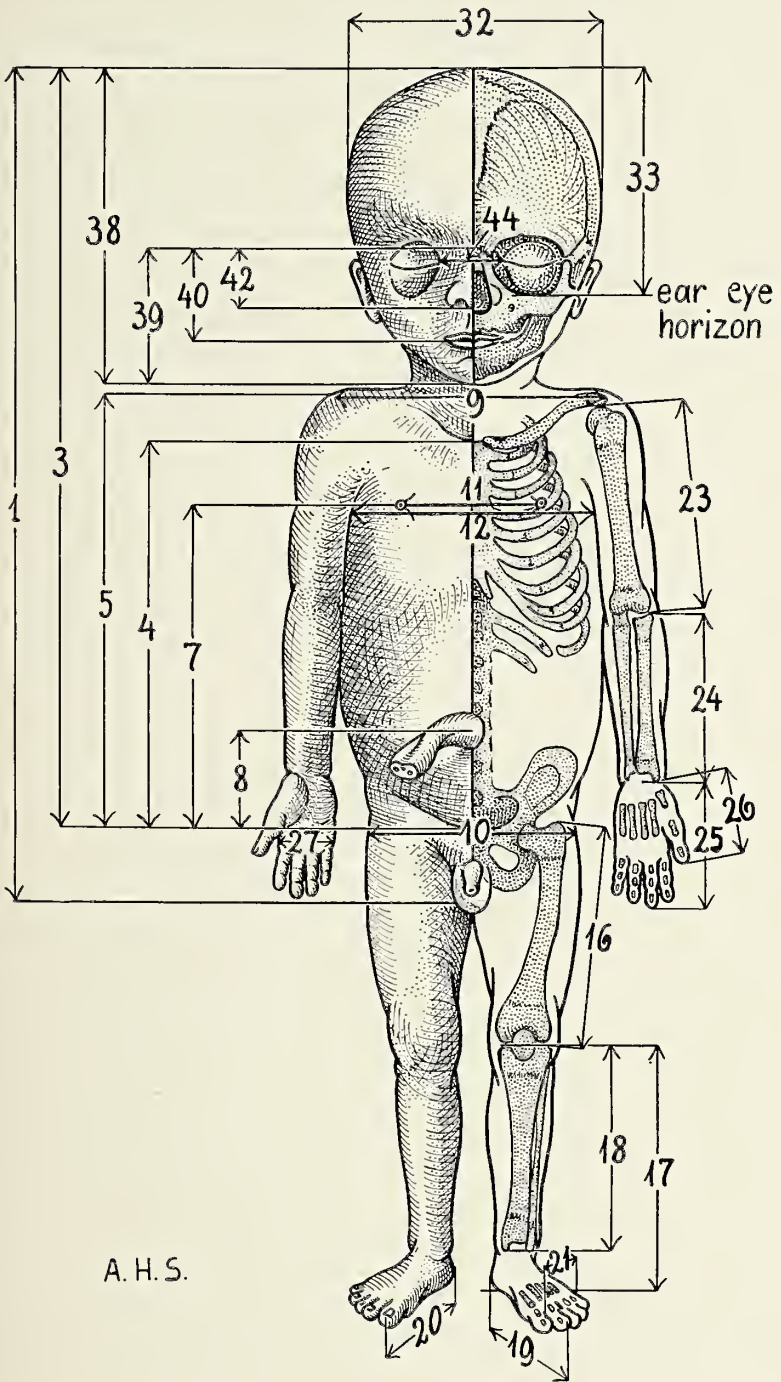
3

(For explanation of plate see opposite page.)

## EXPLANATION OF PLATE III.

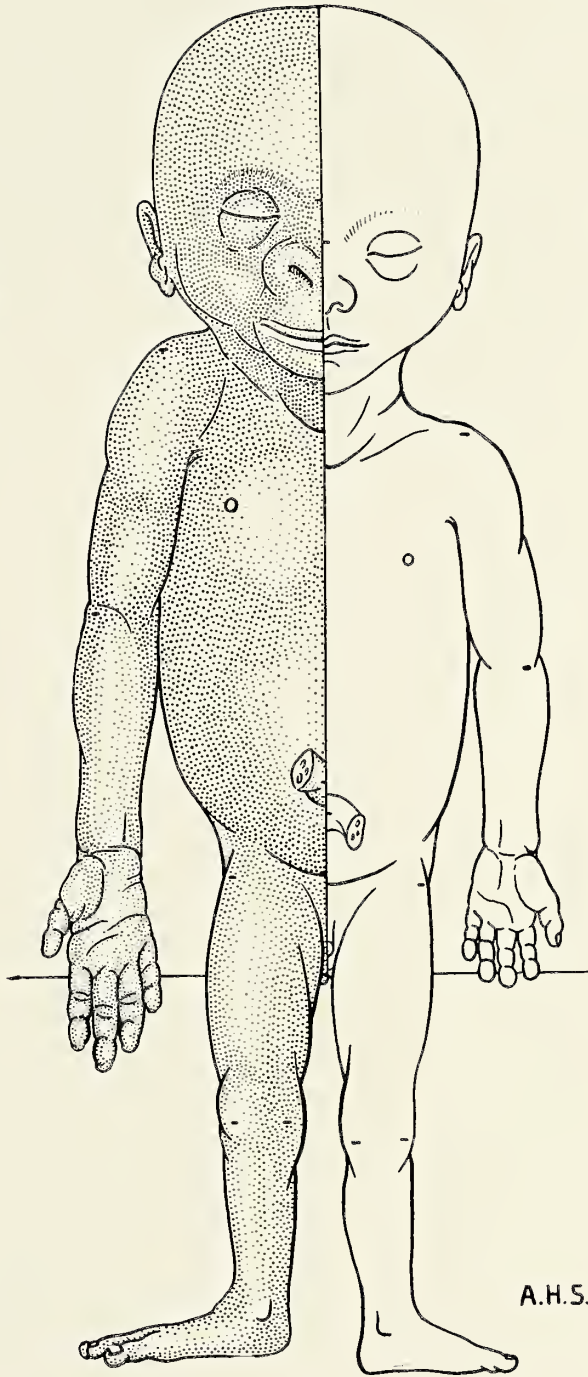
FIG. 1. Diagram of measurements. Human fetus with parts of skeleton shown on one-half of the body. The numbers refer to the serial number of the particular measurements.

FIG. 2. Diagrammatic representation of exact body proportions of Gorilla Fetus II (gray half) and of average proportions of human fetuses (series 1) of corresponding development (white half). The horizontal line marks the lower end of the sitting height. The figure is based upon the measurements in Table 1.



A.H.S.

1



A.H.S.

2

(For explanation of plate see opposite page.)

## EXPLANATION OF PLATE IV.

FIG. 1. Front views of heads of juvenile gorilla (after Klaatsch, 1911) and of juvenile chimpanzee\* (Collection of Department of Anatomy, Johns Hopkins University).

FIG. 2. Perineal region of the female Gorilla Fetus II and of a female human fetus of corresponding development. 1 = clitoris; 2 = labia majora; 3 = anus; 4 = coccygeal tubercle.

FIG. 3. Developmental changes in the external female genitalia of gibbon. *A* = fetus of *Hylobates mülleri*, sitting height 100 mm.; *B*. = fetus of same species, sitting height 161 mm.; *C*. = nearly fullgrown *Hylobates agilis*. 1 = clitoris; 2 = labia minora; 3 = labia majora; 4 = anus; 5 = ischial callosity.

\* This chimpanzee, after its death, was generously sent to the author by its former owner, Mr. J. L. Buck. It is a rather unique specimen, the species of which could not be determined. It has a very broad conspicuous nose of a light blueish-gray color, very long and dense black hair, and unusually short limbs. In a recent article (1927) Mr. Buck mentions this specimen under the name "Bosambo" and expresses the opinion that it is a gorilla-chimpanzee hybrid. However, a careful study of the preserved animal leaves no doubt that it is a true chimpanzee, but perhaps, of a new species.

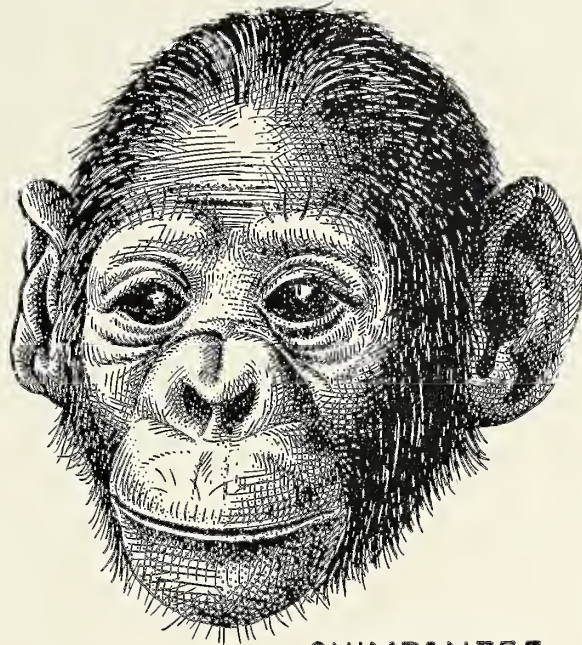
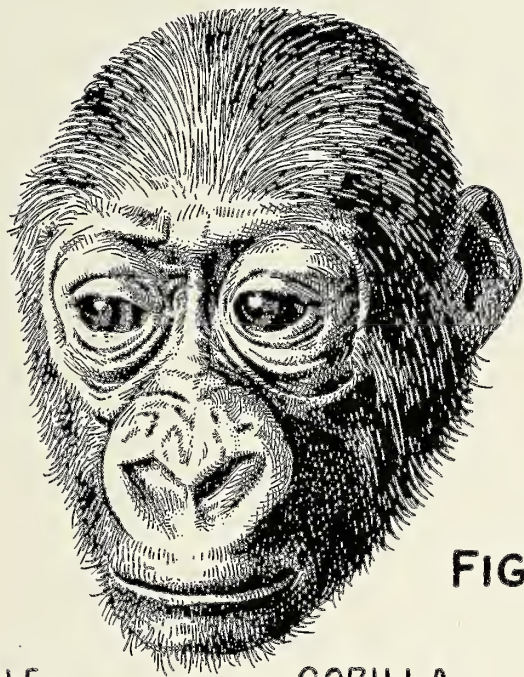
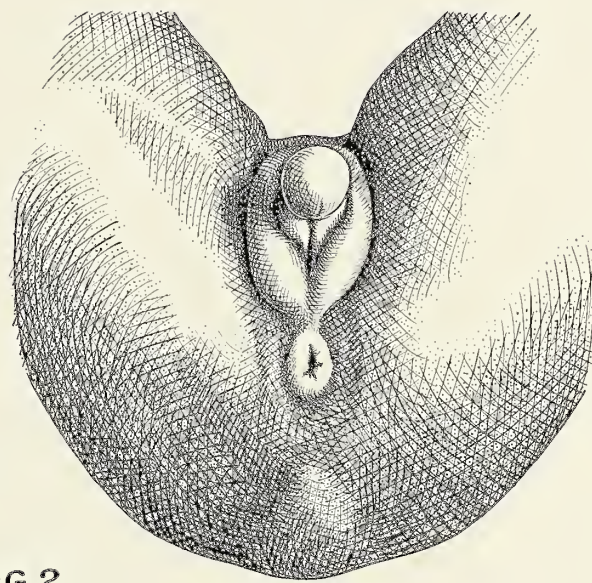
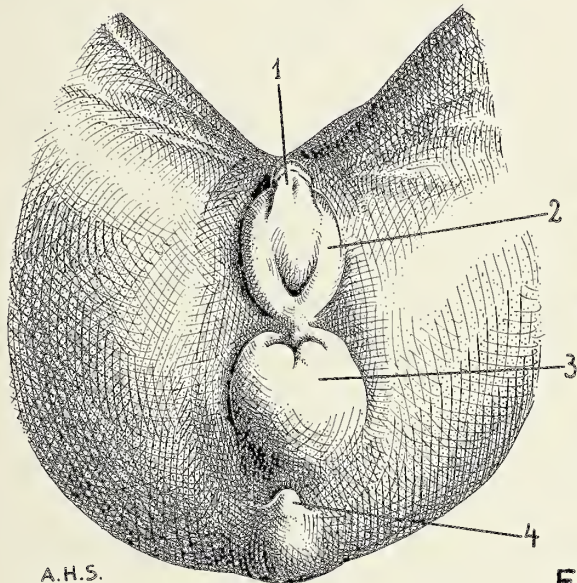


FIG. 1

A.H.S.

GORILLA

CHIMPANZEE

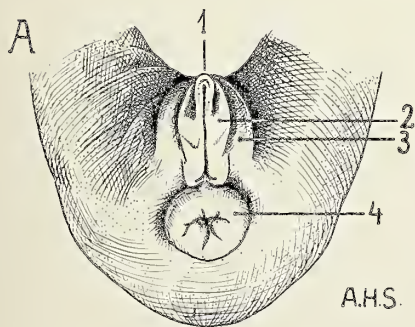


A.H.S.

FIG. 2

GORILLA, ♀

MAN, ♀



A.H.S.

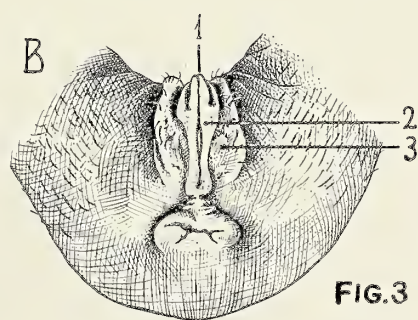
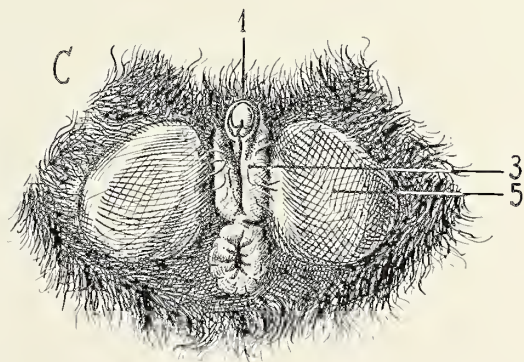


FIG. 3

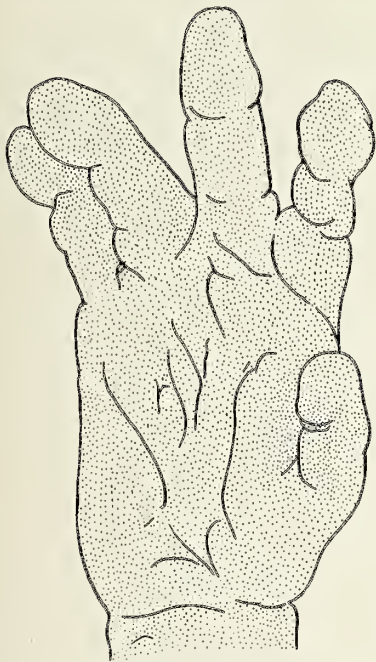


(For explanation of plate see opposite page.)

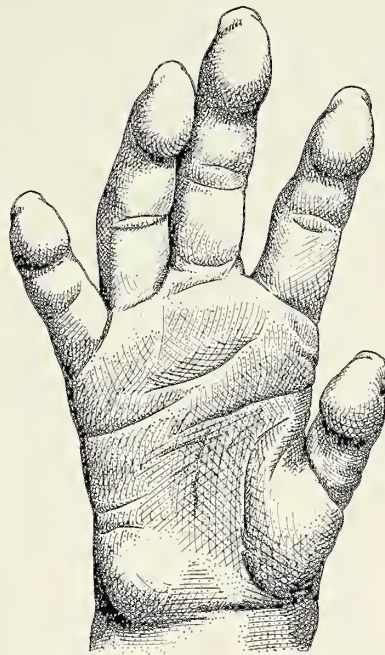
## EXPLANATION OF PLATE V.

Hands of gorilla, all reduced to the same total length. Upper row: fetuses I, II, and III; lower row: adult *G. Gorilla* after Hartmann (1880) and adult *G. beringei* (♀), drawn from a copy of a plaster cast, of which the original was made and published by Akeley (1923).

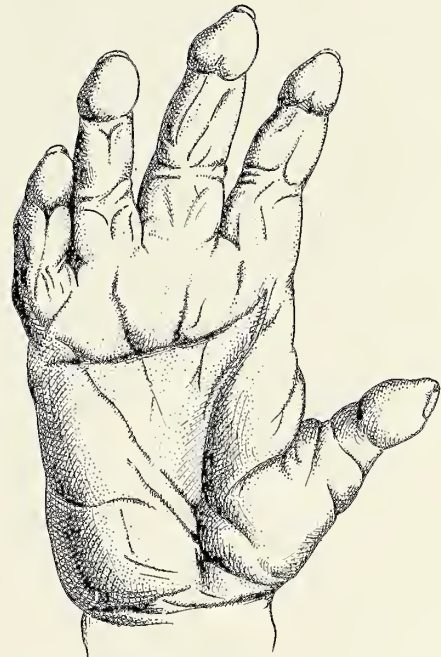




I. (DUCKWORTH)



II. (SCHULTZ)

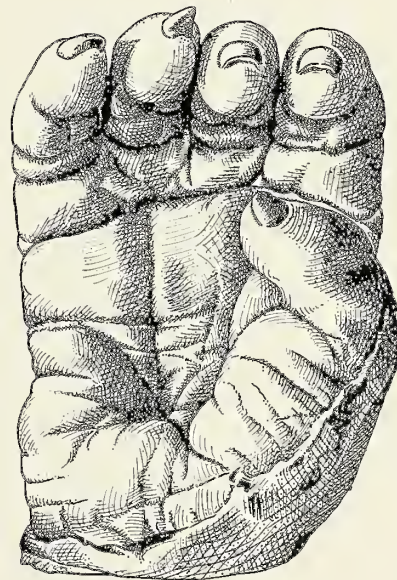


III. (DENIKER)



A.H.S.

ADULT (HARTMANN)

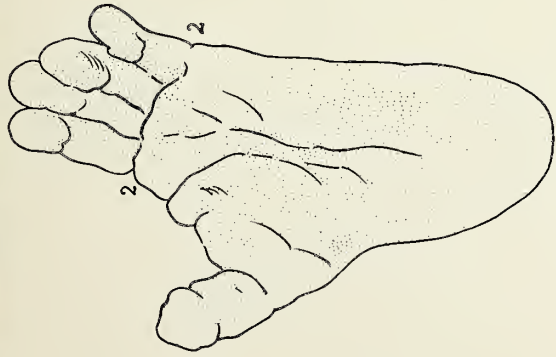


ADULT (AKELEY)

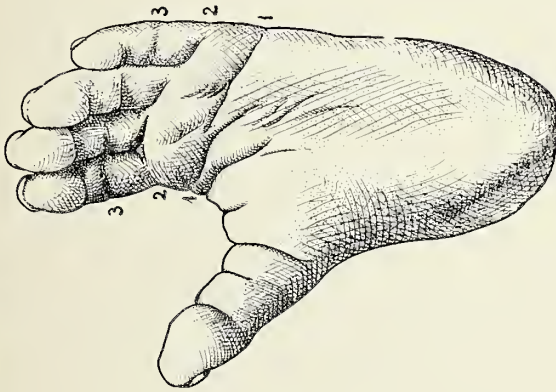
(For explanation of plate see opposite page.)

## EXPLANATION OF PLATE VI.

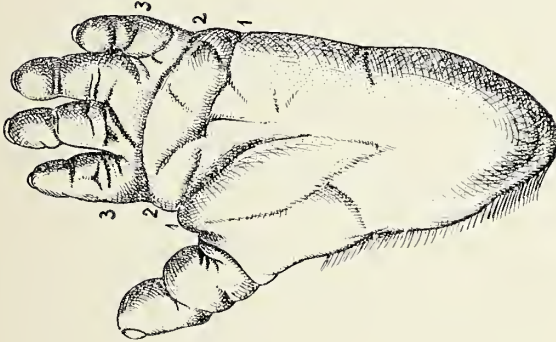
Feet of gorilla, all reduced to the same total length. Upper row: fetuses I, II, and III, five year old male (drawn from a cast of "John Daniel I" by Prof. McGregor), and adult *Gorilla gorilla* (after Hartmann, 1880); it is possible that this gorilla is not entirely adult. Lower row, *left*: feet of negro fetuses of the fifth month, showing the maximum and the minimum relative toe-length of a considerable series of specimens: *right*: adult female *Gorilla beringei* (drawn from a copy of a plaster cast of which the original was made and published by Akeley, 1923) and adult *Gorilla gorilla* (after Brehm, 1876). Distance  $A_1-B$  or  $A-B$  = length of cleft between toes I and II; distance  $A-C$  = total foot-length; 1, 2, and 3 = flexure folds, for explanation of which see text.



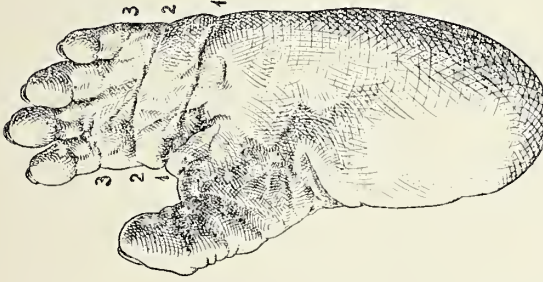
I. (DUCKWORTH)



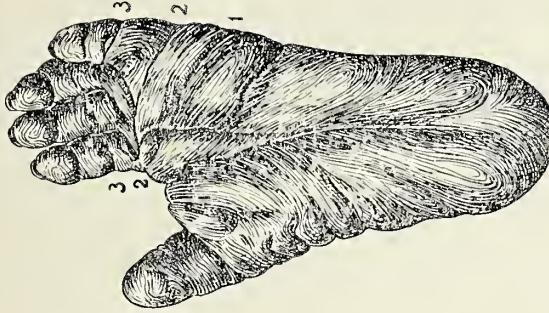
II. (SCHULTZ)



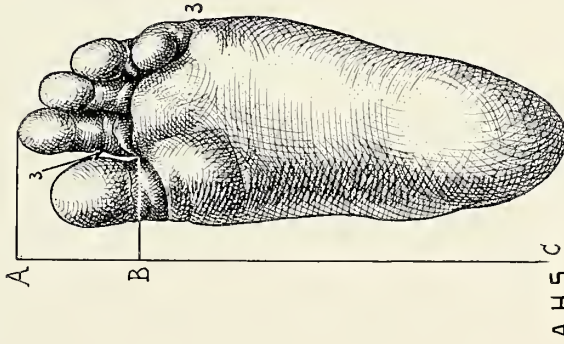
III. (DENIKER)



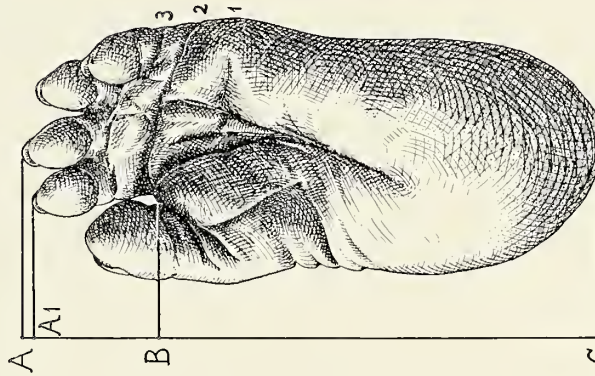
5 YEARS OLD



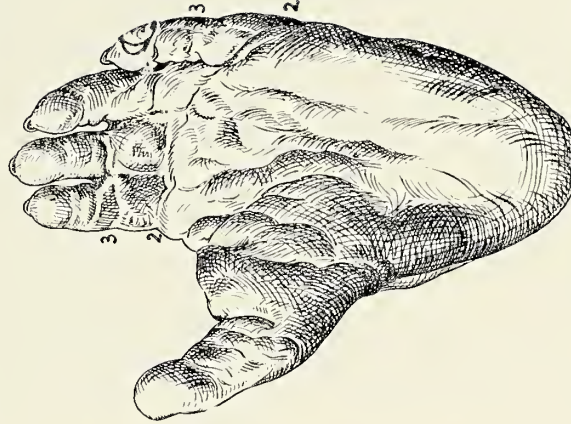
ADULT (HARTMANN)



HUMAN FETUSES, 5TH MONTH



ADULT (AKELEY)



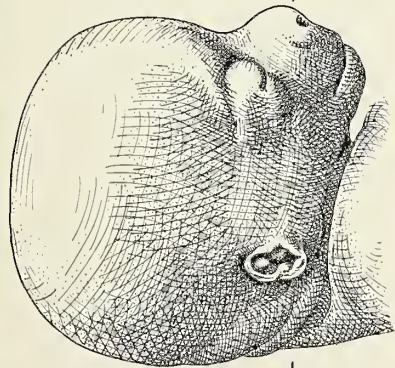
ADULT (BREHM)

(For explanation of plate see opposite page.)

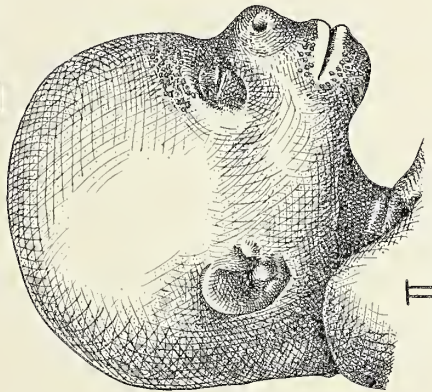
## EXPLANATION OF PLATE VII.

FIG. 1. Side views of heads, all reduced to approximately the same size and oriented according to their ear-eye horizons (the head of Deniker's fetus is probably slightly tilted to the specimen's left side). Upper row: gorilla fetuses I to IV. Lower row: negro fetuses (I corresponding in development to gorilla fetus I; II corresponding to gorilla fetus II) and infantile gorilla (after photograph).

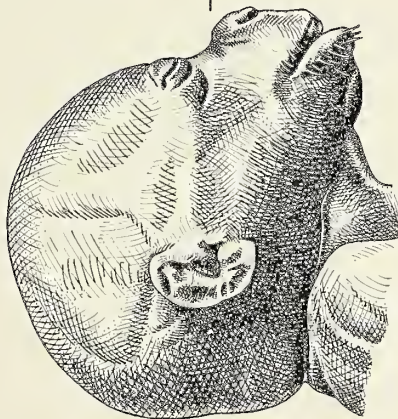
GORILLA FETUSES



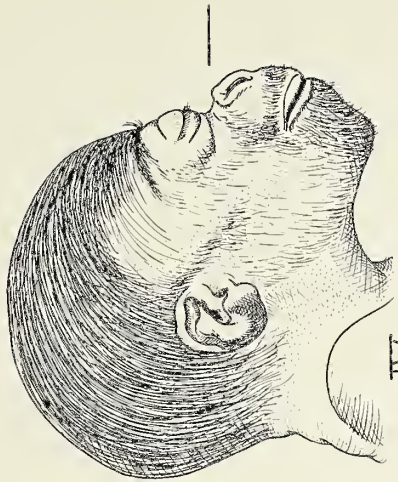
I.  
(DUCKWORTH)



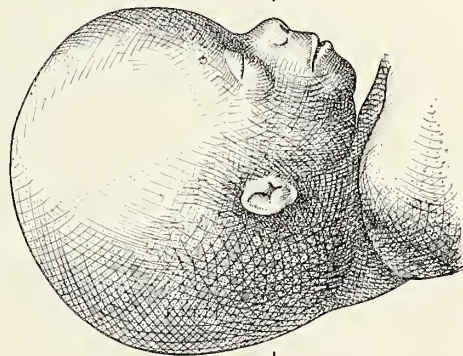
II.  
(SCHULTZ)



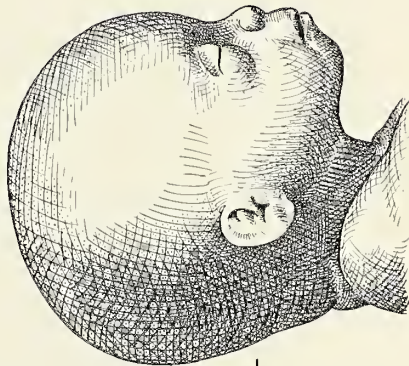
III.  
(DENIKER)



IV.  
(BOLK)

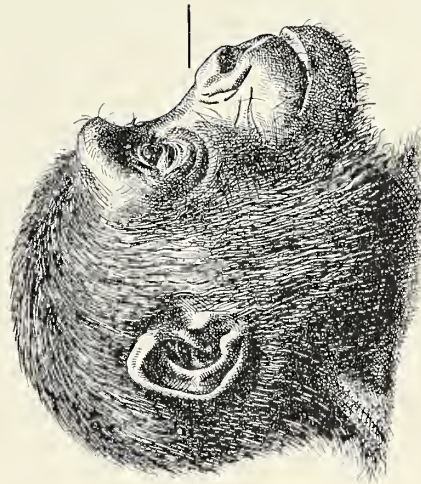


A.H.S.  
I.



II.

NEGRO FETUSES



GORILLA INFANT

— EAR-EYE HORIZON —

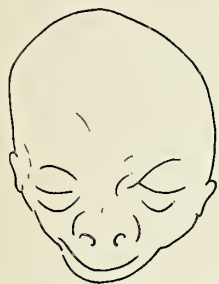
(For explanation of plate see opposite page.)

## EXPLANATION OF PLATE VIII.

FIG. 1. Front views of heads of anthropoid fetuses and infants, all reduced to approximately the same size. Upper row: gorilla fetuses I to IV and infant VI. Lower row: chimpanzee fetus (No. 2, chapter 2), orang fetuses (from the collection of the U.S. National Museum), newborn chimpanzee (after Blair, 1920). The fetuses in the lower row correspond in development approximately to the fetuses perpendicularly above them in the upper row. Judging by the high position of the ears, the heads of fetuses I and IV are tilted forward.

FIG. 2. Front views of skulls of juvenile and adult apes and man (oriented in Frankfort horizon and drawn with dioptrograph). The juvenile and the adult chimpanzee are males; the adult gorilla is a female; the adult negro skull comes from eastern Senegal and is that of a female; the adult white skull is that of a male Swiss Alpine. The two gorillas belong to the collection of the Anthropological Laboratory of the Johns Hopkins University; all the other skulls are in the author's private collection. The thick curves, marked *a* and *b*, represent horizontal sections through the nasal region at the levels indicated by straight lines (*a* and *b*) on the front views of the skulls. Level *a* is determined by the fronto-maxillary suture; level *b* by the lower end of the nasal bones. The section curves were drawn with Martin's diagraph (Martin, 1914) and enlarged to twice the scale of the front views of the skulls. The orbital portions of the curves (*a*) are drawn in thinner lines than the interorbital part.

GORILLA



I. (DUCKWORTH)



II. (SCHULTZ)



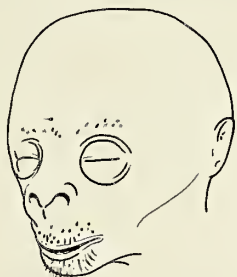
III. (DENIKER)



IV. (BOLK)



2 MONTHS (REICHENOW)



A.H.S.

CHIMPANZEE (FRIEDENTHAL)

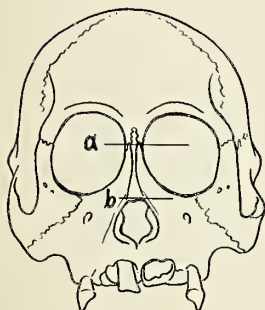


ORANG-UTAN (SCHULTZ)

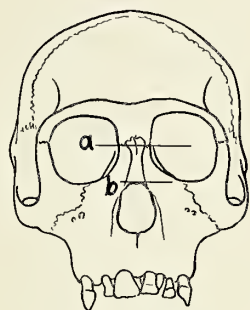


CHIMPANZEE (BLAIR)

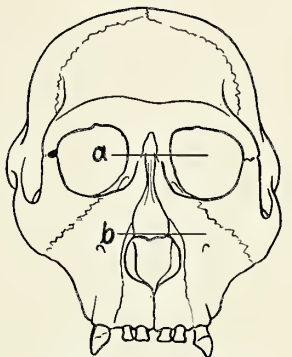
1



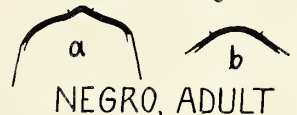
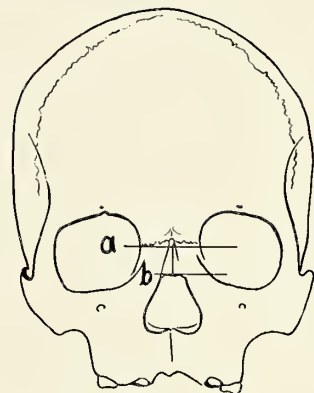
ORANG, JUVEN.



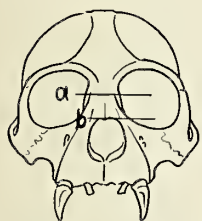
CHIMPANZEE, JUVEN.



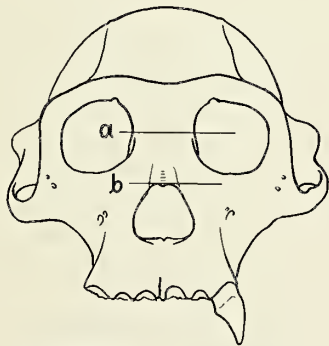
GORILLA, JUVEN.



NEGRO, ADULT



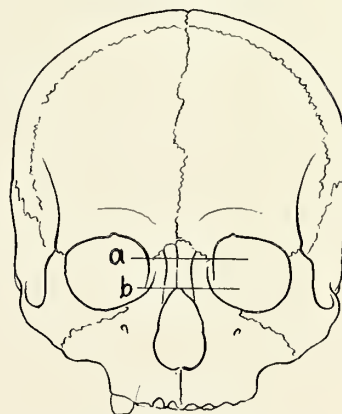
SIAMANG, ADULT  
A.H.S.



CHIMPANZEE, ADULT



GORILLA, ADULT



WHITE, ADULT

2

(For explanation of plate see opposite page.)